Egg Shape in Birds

Jamie Edward Thompson

A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy by Publication

The University of Sheffield

Faculty of Science

Department of Animal and Plant Sciences

March 2020

For always providing a positive mindset when it
comes to discussing my goals and aspirations

For always being the one to say ‘you can’ and
‘you will’

This is for you Nanna.

Contents

Appendices

Summary

Birds demonstrate incredible intra- and interspecific diversity in various egg traits. In particular, there is considerable diversity in egg shape across bird species from nearly spherical to extremely pyriform (pointed) eggs. This variation in avian egg shape has long fascinated researchers and numerous efforts have been made to quantify egg shape traits and examine the possible evolutionary drivers and functions of the observed patterns of avian egg diversity. Previous studies have attempted to examine egg shape at various taxonomic scales and the evidence from these studies collectively suggest that avian egg shape diversity might be driven by two main sources: (i) indirect selection via anatomical constraints or life history trait changes, and/or (ii) direct adaptive selection during the incubation period. However, it is still unclear as to how important these drivers of egg shape diversity are and how their importance might alter at different taxonomic scales. Furthermore, current studies on avian egg shape lack a universally agreed method of accurately quantifying all egg shapes, which makes comparing studies and assimilating overall patterns of egg shape diversity challenging.

This thesis presents published work that aims to contribute further to the understanding of avian egg shape diversity. Firstly, the thesis presents a paper highlighting a novel automated image analysis method that more accurately quantifies egg shape, compared to previous modelling methods, that could be used by all future studies. Second, the thesis presents several papers examining the adaptive function of the extremely pyriform egg of the Common Guillemot (*Uria aalge*). In these papers, evidence is presented that brings in to question the plausibility of the previously popular 'rolling-in-an-arc' adaptive explanation. Instead, three new alternative adaptive hypotheses for the Common Guillemot's pyriform egg are presented: (i) mechanical damage prevention/limitation; (ii) faecal-debris contamination limitation, and (iii) increased stability. Based on current available evidence, it is concluded that the stability hypothesis is currently the strongest supported adaptive explanation for the Common Guillemot's pyriform egg shape. Thirdly, the thesis presents a published paper that looked to examine potential drivers of egg shape patterns at a broader taxonomic scale. Here, the paper examined patterns of egg shape in alcids (Alcidae) and penguins (Spheniscidae), two taxa containing species with considerable variations in egg shape and incubation environments and behaviours. In the study, evidence is presented that highlights the importance of incubation site characteristics as a driver of egg shape variation, something not evident in some other studies at broader taxonomic scales.

Acknowledgements

To be able to work under the guidance of a world-renowned ornithologist like Professor Tim Birkhead is an incredible and exciting opportunity, and I have been very lucky to have had that opportunity for over a decade. It is never dull doing research with Tim, and I have learnt a great amount about what it takes to be a successful researcher through him. Tim has always been supportive, encouraging and constructively critical, and is the person who opened the door of opportunity that gave me the chance to write this PhD thesis. Thank you, Tim, for your unwavering support, for believing in my capabilities as a researcher, and for taking this Yorkshire lad to places I would likely not have ever had opportunities to see. I will always be forever grateful and remember those times together on the guano-covered guillemot ledges of Skomer Island with great fondness.

I have also been incredibly lucky to have learnt under the guidance of Dr Nicola Hemmings. Your support and encouragement during my undergraduate and working days at The University of Sheffield has been pivotal in making me the researcher I am today. Thank you for this continued support and guidance, for being a great scientific role model, and for trusting me with providing assistance on some of your PhD work all those years ago!

During my time as a research technician at The University of Sheffield, I have been incredibly lucky to work with many great people that have made various research projects fun and thought-provoking. Particularly, whilst researching all things eggs, both Dr Duncan Jackson and Dr Marie Attard have provided invaluable assistance and stimulating discussions that has helped shape my research. I am also incredibly grateful to have had the opportunities to work with some great collaborators from other departments and institutions, including Professor John Biggins (School of Mathematics and Statistics, The University of Sheffield) and Professor Bob Montgomerie (Queen’s University, Ontario). Thanks to all the collaborators for their vital contributions to the work presented in this thesis and for providing me with opportunities to learn a great deal from them.

I would like to take the opportunity to thank all the museum curators who have allowed myself and Tim to measure and photograph eggs from their collections, including: Julian Carter and Jennifer Gallichan (The National Museum of Wales); Henry McGhie and Rachel Petts (Manchester Museum);

Professor Robert Barrett (Tromsø University Museum); Professor Jon Fjeldså (Natural History Museum of Denmark), and Dan Gordon (Tyne and Wear Archives and Museums). Special thanks, in particular, go out to Douglas Russell (Natural History Museum at Tring) who has continued to provide invaluable support and access to the Natural History Museum's egg collections throughout the entirety of this research project – I am incredibly grateful for your tireless assistance and forever amazed by your stories about the collections. Thanks also goes out to The Wildlife Trust of South and West Wales, particularly Lizzie Wilberforce and previous Skomer Island wardens Birgitta Büche and Edward Stubbings, for supporting our research on Skomer Island. Natural Resources Wales provided their permission and necessary licencing for us to undertake research on Common Guillemot and Razorbill eggs on Skomer Island, for which I am grateful for. I would also like to thank Dr Julie Riordan, Dr Jodie Crane and Dr Elspeth Kenny who have all provided assistance with fieldwork at various times and, all of which, have made fieldwork that more enjoyable over the years.

Whilst writing this thesis, I have received critical feedback from Tim, Nicola and Dr Kathryn Maher that has allowed me to dramatically improve my thinking, clarity and writing skills, for which I thank them all for.

Thanks to 'The Lunch Bunch' for their amazing friendship and laughter they bring to every work day.

Throughout my pursuits in scientific research, my family has always been my rock. Always supporting and encouraging me. Always interested to hear how I am getting on. Always there when I have the inevitable emotional wobble. I am forever grateful and thankful for everything you do for me, and inspired by you all. My love and thanks to you all, always.

Finally, all my thanks and love must go to my partner Katy. You have always believed that I could do something like this, when I have often doubted it. Thank you for always looking out for me, for being there during the highs and lows of research life, and for being the person I can always confide in. You are a golden egg who makes my life that much more colourful and happier.

The work presented in this thesis would not have been possible without The Leverhulme Trust Grant (RPG-2015-221) awarded to Professor Tim Birkhead.

Declaration

I, the author, confirm that the Thesis is my own work, except where work that has formed part of jointly authored publications has been included. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). All work, except that in **Chapter 6**, has not been previously presented for an award at this, or any other, university. Work in **Chapter 6** has also been previously presented in a PhD thesis entitled *'The adaptive significance of avian eggshell architecture'* by Duncan Jackson, a co-author on the published article, submitted to The University of Sheffield in December 2019.

Acknowledgement of previously published work and currently in press papers presented in the thesis

Chapter 2 was published in Ecology and Evolution:

> **Biggins, J. D., Thompson, J. E. and Birkhead, T. R.** (2018). Accurately quantifying the shape of birds' eggs. *Ecology and Evolution*, **8**, 9728-9738.

Article posted online on the 5th September 2018 and the final version was published in October 2018.

Access the originally published version at:

https://onlinelibrary.wiley.com/doi/10.1002/ece3.4412

Chapter 3 was published in Archives of Natural History:

> **Birkhead, T. R. and Thompson, J. E.** (2019). Wade's Birds of Bempton Cliffs and his observations on Guillemot (*Uria aalge*) eggs. *Archives of Natural History*, **46**, 240-252.

Article posted online September 2019 and the final version was published in October 2019.

Access the originally published version at:

https://www.euppublishing.com/doi/10.3366/anh.2019.0588

This published article has been reproduced in this thesis with the permission of Edinburgh University Press Limited through PLSclear (PLSclear Ref No: 32265).

Chapter 4 was published in Journal of Ornithology:

> **Birkhead, T. R., Thompson, J. E. and Biggins, J. D.** (2017). Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: not a rolling matter? *Journal of Ornithology*, **158**, 679-685.

Article posted online on the 17th February 2017 and the final version was published in July 2017.

Access the originally published version at:

https://link.springer.com/article/10.1007/s10336-017-1437-8

Chapter 5 was published in Ibis:

Birkhead, T. R., Thompson, J. E., Jackson, D. and Biggins, J. D. (2017). The point of a Guillemot's egg. *Ibis*, **159**, 255-265.

Article posted online on the 23rd February 2017 and the final version was published in April 2017.

Access the originally published version at:

https://onlinelibrary.wiley.com/doi/full/10.1111/ibi.12458

This published article has been reproduced in this thesis with the permission of John Wiley and Sons through Copyright Clearance Centre's RightsLink service (License No: 4750680905224), as indicated by Wiley Online Library's Permissions statement:

https://onlinelibrary.wiley.com/page/journal/1474919x/homepage/permissions.html

Chapter 6 was published in Journal of Experimental Biology:

Jackson, D., Thompson, J. E., Hemmings, N. and Birkhead, T. R. (2018). Common guillemot (*Uria aalge*) eggs are not self-cleaning. *Journal of Experimental Biology*, **221**, jeb188466.

Article posted online on the 15th October 2018 and the final version was published on the 27th November 2018.

Access the originally published version at:

http://jeb.biologists.org/lookup/doi/10.1242/jeb.188466

No permission is required to include this published work in this thesis, as indicated by The Journal of Experimental Biology's copyright policy: https://jeb.biologists.org/content/rights-permissions also see relevant user licence https://www.biologists.com/user-licence-1-1/

Chapter 7 was published in The Auk:

Birkhead, T. R., Thompson, J. E. and Montgomerie, R. (2018). The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *The Auk*, **135**, 1020-1032.

Article posted online on 22nd August 2018 and the final version was published on the 1st October 2018.

Access the originally published version at:

https://academic.oup.com/auk/article/135/4/1020/5149021

No formal permission is required to include this published work in this thesis, as indicated by Oxford University Press's Author Reuse and Self-Archiving online statement:

https://global.oup.com/academic/rights/permissions/autperm

Chapter 8 was published in Ibis:

> **Birkhead, T. R., Thompson, J. E., Biggins, J. D. and Montgomerie, R.** (2019). The evolution of egg shape in birds: selection during the incubation period. *Ibis*, **161**, 605-618.

Article posted online on 20th August 2018 and the final version was published in July 2019.

Access the original article at:

https://onlinelibrary.wiley.com/doi/full/10.1111/ibi.12658

This published article has been reproduced in this thesis with the permission of John Wiley and Sons through Copyright Clearance Centre's RightsLink service (License No: 4750681428711), as indicated by Wiley Online Library's Permissions statement:

https://onlinelibrary.wiley.com/page/journal/1474919x/homepage/permissions.html

Appendix 2 presents a recently published paper in British Birds:

> **Birkhead, T.R., Jensen, J-K, Thompson, J.E., Hammer, S., Thompson, P. & Montgomerie, R.** (2020). Two-egg clutches in the Fulmar. *British Birds*, **113**, 165-170.

Access the original article at:

https://britishbirds.co.uk/article/two-egg-clutches-in-the-fulmar/

This published article has been reproduced in this thesis with direct permission from Roger Riddington, editor of British Birds.

Appendix 3 presents a recently accepted short communication to be published in Ibis:

> **Birkhead, T. R., Russell, D. G. D., Garbout, A., Attard, M. R. G., Thompson, J. E. and Jackson, D.** (2020). New insights from old eggs – the shape and thickness of Great Auk *Pinguinus impennis* eggs. *Ibis*, **Early view**, doi: 10.1111/ibi.12820.

Article posted online on 26th February 2020.

Access the original article at:

https://onlinelibrary.wiley.com/doi/10.1111/ibi.12820

This in press article has been reproduced in this thesis with the permission of John Wiley and Sons through Copyright Clearance Centre's RightsLink service (License No: 4776440698461), as indicated by Wiley Online Library's Permissions statement:

https://onlinelibrary.wiley.com/page/journal/1474919x/homepage/permissions.html

CHAPTER 1:

Introduction

1.1. Background

Thomas Wentworth Higginson once wrote: '*I think that, if required on pain of death to name instantly the most perfect thing in the universe, I should risk my fate on a bird's egg*' (Higginson 1862: 368-369). Indeed, the avian egg is of remarkable biological design and architecture – a product of numerous key evolutionary adaptations beginning over 360 million years ago when ancestral vertebrates first expanded to non-aquatic habitats (Sumida & Martin 1997; Reisz & Müller 2004; Sander 2012). An initial pivotal evolutionary innovative adaptation was the development of an amniotic egg, characterised by specialised membrane and shell structures, thought to have first arisen around 310 million years ago (Reisz & Müller 2004; Sander 2012). Amongst many other subsequent species-specific adaptations to novel selection pressures and/or constraints, the development of the amniotic egg was critical to the successful colonisation of a variety of non-aquatic habitats (Sander 2012; D'Alba et al. 2017; Stoddard et al. 2017) and, therefore, the remarkable diversification of all land-based amniotes, including birds (Sander 2012). It is, however, the avian egg that perhaps, above all, exemplifies the most successful egg architecture, as the specific evolution of a hard-calciferous eggshell has allowed for particularly incredible diversification of birds across all environmental extremities (Deeming 2002; del Hoyo 2020).

The avian egg essentially acts as a self-sustaining vessel for embryo development (Birkhead 2016), which ultimately results in the successful hatching of new progeny. The general components of avian eggs include: (i) the ovum, containing the germinal disc (the embryo-forming portion of the egg) and nutrient-rich yolk; (ii) the albumen, the shock-absorbing semifluid that envelops and supports the ovum, and (iii) the proteinaceous eggshell membranes and (iv) calcified eggshell, which both encase the inner contents (Romanoff & Romanoff 1949). Collectively, these components provide the necessary food, water and other nutrients; facilitation of respiratory gas exchange and conservation of water, and protection against physical damage and/or microbial infection essential for healthy embryonic growth and hatching of new progeny (Romanoff & Romanoff 1949; Board & Fuller 1974; also see Birkhead 2016).

Despite all avian eggs consisting of these general components, there is considerable intra- and interspecific diversity in these traits across all birds (Romanoff & Romanoff 1949; Tyler 1969; Board 1982; Deeming 2002; Birkhead 2016). For instance, the relative proportion of yolk to albumen (e.g. Tarchanoff 1884; Romanoff & Romanoff 1949; Ar & Yom-Tov 1978; Carey et al. 1980; Sotherland &

Rahn 1987), the nutritional composition of yolk (e.g. Ricklefs 1977; Carey et al. 1980) and antimicrobial protein content and/or concentration within albumen (e.g. Saino et al. 2007; Shawkey et al. 2008; Wellman-Labadie et al. 2008) can all vary across the eggs of different bird species. Eggshell thickness (e.g. Schönwetter 1960-1992; Ar et al. 1979), porosity (e.g. Board et al. 1977; Tullett & Board 1977; Board & Scott 1980; Ar & Rahn 1985) and microstructures (e.g. Board 1982; Mikhailov 1997; D'Alba et al. 2014, 2016, 2017) also vary across bird species. Furthermore, avian eggshells show remarkable diversity in both colour and patterning (Wallace 1889; Gaston & Nettleship 1981; Kilner 2006; Cassey et al. 2010; Cherry & Gosler 2010; Stevens 2011; Birkhead 2016).

Variation across bird species in egg components are likely to be a product of life history strategies (e.g. Ricklefs 1977; Ar & Yom-Tov 1978; Carey et al. 1980; Sotherland & Rahn 1987) and/or adaptive optimisation to the breeding behaviours and environments that eggs are exposed to (Board 1982; Deeming 2002; Cherry & Gosler 2010; Birkhead 2016; D'Alba et al. 2016). Variation in the relative proportion of yolk to albumen, lipid content of the yolk and water content of eggs can often be attributed to developmental mode (i.e. altricial-precocial chick development spectrum; Nice 1962) life history strategies (e.g. Ricklefs 1977; Ar & Yom-Tov 1978; Carey et al. 1980; Sotherland & Rahn 1987; Vleck & Vleck 1987). The variation in eggshell thickness across birds' eggs has been shown to be related to initial egg mass (e.g. Ar et al. 1974, 1979; Rahn & Paganelli 1989; Birchard & Deeming 2009) and, in turn, incubating body mass (e.g. Birchard & Deeming 2009; Juang et al. 2017), as well as incubation environments and behaviour (e.g. Arad et al. 1988; Rahn et al. 1988; Birchard & Deeming 2009; Stein & Badyaev 2011). Microstructures such as the 'shell accessory material' (Board et al. 1977; Board & Scott 1980), often referred to as the 'cuticle', found on the eggshell surface have been shown to be adaptive for waterproofing (Board & Halls 1973a, 1973b; Sparks & Board 1984), antimicrobial protection (D'Alba et al. 2014; Gole et al. 2014a, 2014b; Ishikawa et al. 2010; Wellman-Labadie et al. 2008), resistance to water loss and desiccation (Deeming 1987; Thompson & Goldie 1990), and protection from harmful wavelengths of light, as a result of changes to eggshell colour and patterning (Lang & Wells 1987; Samiullah & Roberts 2014; Maurer et al., 2015; Lahti & Ardia 2016). Given these numerous adaptations, interspecific variations in shell accessory material across birds' eggs are thus likely to be adaptations to specific breeding environments (Board 1982; D'Alba et al. 2016). Studies on avian eggshell colour and patterning have proposed a number of adaptive explanations for observed diversity including (see Underwood & Sealy 2002; Kilner 2006; Cherry & Gosler 2010): crypsis (Wallace 1889; Lack 1958), brood parasitism and host dynamics (i.e. brood parasite mimicry and host egg recognition; Newton 1896; Kilner 2006; Spottiswoode & Stevens 2010; Stoddard & Stevens 2011), aposematism (Swynnerton 1916), thermoregulatory benefits (Wisocki et al. 2020), UV wavelength protection (Montevechi 1976; Maurer et al. 2015; Lahti & Ardia 2016), colonial breeding egg recognition (Tschanz 1959; Birkhead 1978; Hauber et al. 2019), sexual selection signalling (Moreno & Osorno 2003; Soler et al. 2005; but see Kilner 2006 and Cherry & Gosler 2010), and eggshell strengthening (Solomon 1987; Gosler 2006).

One particular egg trait that exhibits notable diversity is shape. Variation in egg shape has fascinated researchers for well over a century (e.g. Hewitson 1831; Thompson 1917; Thomson 1964; Stoddard et al. 2017; see Birkhead 2016). Specifically, researchers have focused on three broad questions relating to avian egg shape: (i) what are the mechanisms of egg shape formation; (ii) how do we accurately quantify egg shape, and (iii) what are the evolutionary drivers of egg shape?

Surprisingly, despite the prolonged interest in avian egg shape, we still know relatively little about how different egg shapes are formed within the oviduct (Birkhead 2016). This lack of understanding is, in part, likely due to the continued absence of suitably developed technologies and methods to effectively examine these mechanistic questions. Hence, research into avian egg shape variation has generally focused on both developing appropriate ways to describe and quantify egg shape diversity (e.g. Mallock 1925; Preston 1953, 1968, 1969; Baker 2002; Deeming & Ruta 2014; Stoddard et al. 2017; Attard et al. 2017, 2018; Biggins et al. 2018), and attempting to understand the potential evolutionary drivers and functions of this diversity (e.g. Andersson 1978; Barta & Székely 1997; Birkhead et al. 2017b, 2018, 2019; Stoddard et al. 2017; Deeming 2018; Duursma et al. 2018). Indeed, there has been a recent increase of studies examining the evolutionary drivers of avian egg shape (e.g. Attard et al. 2017; Birkhead et al. 2017b, 2018, 2019; Stoddard et al. 2017; Deeming 2018; Duursma et al. 2018; Hays & Hauber 2018; Shatkovska et al. 2018).

Below, I review the current research literature on avian egg shape diversity. First, I review the progress made in describing and quantifying egg shape. Second, I examine the potential drivers of egg shape diversity as suggested by the current literature. Finally, I present an overview of research examining the potential adaptive benefits of the unique pyriform-shaped (i.e. pear-shaped or pointed) egg of the Common Guillemot *Uria aalge*.

1.2. Avian Egg Shape

1.2.1 Describing and quantifying egg shape

Traditionally, birds' eggs have been categorised into several descriptive shape classes. Examples of descriptive terms previously used to classify avian egg shapes include 'spherical', 'oval', 'elliptical', 'bi-conical', 'elliptical ovate', and 'pyriform' (Thomson 1964; also see Birkhead 2016), and Walters (1994) suggested that there are in total eight typical egg shapes. However, this simplistic, qualitative approach to categorising egg shape types, whilst perhaps initially useful, does not allow for the more subtle intra- and interspecific differences in egg shape. In fact, these traditional categorisations of egg shape are very loose since shapes seen in many species often overlap (Birkhead 2016). Indeed, it is now appreciated that egg shapes within birds fall across a continuum, with no apparent divisions between traditionally described shape classes (e.g. Stoddard et al. 2017). It has also been argued that traditional categorisations of egg shape are uninformative and, sometimes, misleading (Mytiai & Matsyura 2019).

Quantifying egg shape mathematically is an alternative approach that enables researchers to better explore differences in egg shape variation across birds, and to avoid the limitations of the traditional egg shape classifications. The development of a single, quantifiable shape index that fully captures all aspects of egg shape traits would be most desirable but, as yet, no such index is available (Birkhead 2016).

Researchers first attempted to mathematically describe avian egg shape during the early to mid-20th Century. However, some authors concluded that it was not possible to mathematically describe all egg shapes (Thompson 1942; Romanoff & Romanoff 1949). However, Preston (1953) subsequently demonstrated the feasibility of effectively capturing the diversity of avian egg shapes using mathematical equations. Using four mathematical parameters, Preston (1953) was able to adequately describe the entire diversity of avian egg shapes and these mathematical insights underpin subsequent studies (e.g. Preston 1968; Todd & Smart 1984; Biggins et al. 2018). However, Preston's (1953) mathematical modelling lacked any biologically intuitive and interpretable measurements of shape and he later attempted to address this issue by identifying three dimensionless shape indices that he felt captured *all* avian egg shape characteristics: 'asymmetry', 'bicone' and 'elongation' (Preston 1968; also see Biggins et al. 2018).

Despite Preston's (1953, 1968, 1969) important breakthroughs in quantifying avian egg shape, there was a notable lack of uptake for such methods (Mänd et al. 1986; Biggins et al. 2018). There are three possible reasons for the lack of use of these methods, despite their evident effectiveness: (i) calculations of two of the three shape indices (asymmetry and bicone) presented in Preston (1968, 1969) required a specially designed, not readily available apparatus (i.e. a spherometer) to measure the curvature at the egg poles (Biggins et al. 2018); (ii) measurements required for Preston's (1968, 1969) shape index calculations were made manually on egg profile images, which is both laborious and impractical for studies depending on large sample, and particularly challenging to use on small eggs (Mänd et al. 1986), and (iii) Preston's (1953, 1968, 1969) formulae were probably considered too complex by researchers unfamiliar with the mathematics (Biggins et al. 2018).

Instead, researchers have typically used two general, simpler shape indices to describe and quantify egg form: [1] *asymmetry*, the extent to which the furthest distance from the maximum egg breadth line to one of the egg poles deviates from the equator (i.e. the points on the egg surface that is equidistant to each egg pole; note that this is different to 'asymmetry' in Preston 1968), and [2] *elongation*, the relative ratio between maximum egg length and maximum egg breadth (see Biggins et al. 2018 for further details). To acquire these indices, mathematical modelling of the egg shape is still required. Besides Preston's (1953, 1968, 1969) there have in fact been a number of alternative modelling methods proposed (e.g. Carter 1968; Carter & Morley Jones 1970; Baker 2002; Troscianko 2014; also see Köller 2020; Biggins et al. 2018).

Many variations of 'asymmetry' and 'elongation' exist within the literature (see Biggins et al. 2018) and, as a result, different studies which use the same indices often refer to them by alternative names, and/or different shape indices are referred to by the same name. This generates confusion and so, in order to improve clarity, it is important that all future studies use a universally agreed set of well-defined and appropriate shape indices.

Another limitation within the current literature is that many of the alternative mathematical modelling methods used by previous studies to obtain egg shape indices are limited in their ability to accurately quantify asymmetry and elongation shape indices, at least for the more extreme egg shapes produced by some alcids and waders (Biggins et al. 2018). In a recent comparative study, for example, Stoddard et al. (2017) used mathematical formulae defined by Baker (2002), which does not accurately quantify shape indices for eggs with a more pyriform shape. Stoddard et al. (2017) recognised this and, as a result, excluded a number of species from their analyses. Obviously, it is essential in large comparative studies, that *all* avian egg shapes are included. Hence, providing easier access to modelling methods, such as Preston's (1953), that are known to produce the most accurate measures of egg shape, would allow the inclusion of previously excluded bird species in future comparative analyses.

Advancements in both digital cameras and automated processing of digital image technologies, provides an opportunity to develop a novel, enhanced method of obtaining shape indices from all birds' eggs, which integrates the mathematical formulae presented by Preston (1953). A number of studies has used digital photography to examine egg shape (e.g. Barta & Székely 1997; Mónus & Barta 2005; Bán et al. 2011; Mityay et al. 2015; Deeming & Ruta 2014; Stoddard et al. 2017). However, these previous studies are limited either through a lack of automated processing, a use of less accurate mathematical shape modelling methods, and/or a lack of clear methods for other studies to adopt (Biggins et al. 2018). In Biggins et al. (2018), presented in Chapter 2 of this thesis, we attempt to address these issues by developing a novel, accessible method for automating egg shape analyses on egg silhouette photographs based on Preston's (1953) modelling methods. Despite recent developments in 3D-shape analysis of avian egg shape (Attard et al. 2018), the fact that eggs are typically axisymmetrical means that 2D-shape analysis methods like Biggins et al. (2018) are perfectly adequate, more practical and more cost effective.

1.2.2. What are the potential drivers of egg shape diversity?

Two approaches have been used to examine the potential drivers of interspecific avian egg shape variation (see Birkhead 2016; Stoddard et al. 2019). First, egg shape diversity might be a passive by-product of indirect selective pressures derived from differing life history traits, typically relating to developmental modes, allometry and anatomical constraints (e.g. Rensch 1947; Warham 1990; Iverson & Ewert 1991; Anten-Houston et al. 2017, Stoddard et al. 2017; Deeming & Mayr 2018; Shatkovska et al. 2018). Second, avian egg shape could also be a product of adaptive fine tuning to direct selective pressures of differing breeding behaviours and/or environments (e.g. Tschanz et al. 1969; Andersson 1978; Ingold 1980; Barta & Székely 1997; Birkhead et al. 2017b, 2018, 2019; Deeming & Mayr 2018; Duursma et al. 2018; Hays & Hauber 2018). In truth, it is likely that both direct and indirect sources of selective pressure drive avian egg shape diversity (Birkhead et al. 2019; Stoddard et al. 2019).

A number of studies have highlighted significant relationships between shape indices such as asymmetry and elongation (see section 1.2.1 for general definitions) and factors such as egg size and adult body mass (e.g. Stoddard et al. 2017; Deeming 2018), with egg size in particular often explaining a large proportion of observed variation in egg shape (e.g. Stoddard et al. 2017). Such relationships might imply that some form of anatomical constraint is largely responsible for driving changes to avian egg shape. Previously, differences in ovum composition and size, in addition to levels of albumen secretion, have been hypothesised to potentially alter the level of physical constraint exerted on eggs by the oviduct, and thus influence their shape (Deeming & Ruta 2014; Deeming 2018). Certainly, the size and composition of birds' eggs vary considerably (Carey et al. 1980; Sotherland & Rahn 1987; Deeming 2007a, 2007b) and are linked to developmental mode (Carey et al. 1980; Sotherland & Rahn 1987). Whilst different developmental modes demonstrate differing typical egg shape (Deeming 2018), these life history traits seem to have little effect on egg shape (Mytiai et al. 2017) and do not explain a significant proportion of egg shape variation in phylogenetically controlled analyses (Deeming 2018). There is, however, some evidence that differences in egg composition have significant effects on egg shape parameters, such as elongation, irrespective of phylogeny or developmental mode (Deeming 2018). However, the overall explanatory power of egg composition on avian egg shape is minimal (Deeming 2018), suggesting other factors might also be driving this variation.

It has also been suggested that avian egg shape variation might be a product of variation in pelvis size and shape across bird species (e.g. Rensch 1947; Warham 1990; Deeming 2018). Pelvis size and shape are related to forms of avian locomotion, which are in turn related to different musculatures and morphological body plans (Anten-Housten et al. 2017). Given this apparent relationship between pelvis traits and locomotory style (Anten-Housten et al. 2017), it is possible that egg shape is a secondary characteristic product of such relationships (Deeming 2018). Indeed, a recent study has provided some support for this hypothesis (Shatkovska et al. 2018).

A recent extensive comparative study by Stoddard et al. (2017) found hand-wing index (Kipp 1959; Lockwood et al. 1998), a proxy of flight ability (Claramunt et al. 2012; Pigot & Tobias 2015; Kennedy et al. 2016), to be a significant predictor of egg shape, after controlling for phylogeny, body size, egg size and a number of other variables relating to incubation and climatic characteristics (see

Supplementary Material in Stoddard et al. 2017). The authors suggested selection for greater flight ability would select for a constrained, muscular and streamlined body plan that in turn directly or indirectly affects egg shape traits (Stoddard et al. 2017). Although Stoddard et al. (2017) showed hand-wing index to be a predictor of egg shape variation, this predictor appeared to explain only about 4% of the total interspecific variance in egg shape. It has been argued that small effect sizes are perhaps to be expected in such broad scale studies (Graham et al. 2018; Stoddard et al. 2019), but nevertheless, it highlights the possibility that other drivers of egg shape variation may play an equally or more important role.

Instead of, or perhaps, as well as considering egg shape variation as a secondary product of life history traits, it is perhaps more plausible that this apparent diversity is a product of natural selection, specifically driven by differing incubation behaviours and/or environments (Hoyt 1976; Deeming & Ruta 2014) – particularly considering that the incubation period (10-60 days; see Rahn & Ar 1974; Ricklefs & Starck 1998; Deeming 2002) is much longer than the brief (< 24 hours) period of egg formation (Birkhead et al. 2019). Deeming & Mayr (2018) suggested that the occurrence of contact incubation in bird evolution is potentially linked to observed changes in egg shape, although whether contact incubation is the primary driver of this change or a consequential adaption after changes to the biometrics of earlier bird ancestors and their egg shape is unclear. Given this observation, one might hypothesise that subtler changes to incubation behaviours and/or breeding site choices in modern bird species are in turn reflected in the observed egg shape diversity. This idea is perhaps supported by previous studies that have proposed that certain egg shapes provide adaptive benefits during incubation including: improved incubation proficiency (Andersson 1978); enhanced optimisation of gas exchange for successful embryo development (Smart 1991); improved shell strength (Bain 1991; Barta & Székely 1997); increased hatchability, particularly in dry environments (Mao et al. 2007), and reduced egg rolling displacement/egg loss for cliff breeding Laridae (Smith 1966) and Alcidae (Tschanz et al. 1969; Ingold 1980; Hays & Hauber 2018; but see section 1.2.3.). A recent comparative analysis of Australian passerines demonstrated that both egg shape and nest structure can be explained by variations in climatic conditions (Duursma et al. 2018). Despite this evidence for egg shape being driven by direct adaptive selection for incubation behaviours and/or environments, Stoddard et al. (2017) found no factors associated with incubation or climatic conditions explained significant variation in avian egg shape when analysed at a broad taxonomic level.

Collectively, previous studies that have examined the possible drivers of avian egg shape diversity so far highlight the likelihood that various selective forces are acting upon egg shape phenotypic diversification with birds (Stoddard et al. 2019). Furthermore, it is likely that the significance and effect size of different potential selective drivers of egg shape diversity will increase or decrease depending on the phylogenetic scale a study chooses to examine (Hall 2011; Graham et al 2018; Stoddard et al. 2019). To gain further clarity and understanding of the various potential drivers of egg shape diversity, it is imperative that studies continue to examine such biological questions at both narrower and broader taxonomic scales.

1.2.3. The case of the Common Guillemot's pyriform egg

The Common Guillemot *Uria aalge* is a colonial seabird that nests directly on bare rock cliff ledges or other equally precipitous breeding habitats (Tschanz et al. 1969; Ingold 1980). Like its closely related sister species, Brünnich's Guillemot *Uria lomvia* (see Gaston & Nettleship 1981), Common Guillemots are known for their diversity in egg traits such as colour, patterning and shape (Tschanz et al. 1969; Birkhead 2016; Birkhead et al. 2017a; Birkhead & Montgomerie 2018; Hauber et al. 2019). Specifically, both *Uria* species are known for their extremely 'pyriform' (i.e. pear-like or pointed) egg shape (Tschanz et al. 1969; Birkhead 1993, 2016; Birkhead et al. 2017a, 2017b; Stoddard et al. 2017), which has intrigued researchers for many centuries (reviewed by Birkhead 2016, 2017).

Many researchers have been intrigued by the potential evolutionary drivers behind the production of extremely pyriform eggs seen in the *Uria* guillemot species and, given their unique breeding habitats and conditions (Tschanz et al. 1969; Ingold 1980), most studies have focused on the possible adaptive benefits of this egg shape during incubation (e.g. Hewitson 1831; Belopol'skii 1961; Tschanz et al. 1969; Ingold 1980; Birkhead et al. 2017a, 2017b, 2018, 2019; Hays & Hauber 2018; reviewed in Birkhead 2016, 2017). Explanations for the shape of Common Guillemot eggs go as far back to William Harvey in the 1600s who suggested that guillemots cemented their eggs on to the cliff to avoid any loss (discussed in Birkhead 2016). Although this was soon realised to be incorrect, much subsequent work focussed on the idea of preventing egg loss from the sloping breeding cliff ledges (see Birkhead 2016).

Pennant (1768) suggested that rather than being glued to the rock, the guillemot’s egg was perfectly balanced on the breeding site and, presumably, he assumed that the pyriform shape allowed for such perfect balance. Hewitson (1831) suggested that, if a guillemot egg was knocked or blown by the wind, its pyriform shape allowed it to act like a spinning top (i.e. spin around its pointed axis) keeping it in its same position, and thus minimise the risk of loss from the breeding ledges. This latter ‘spin-like-a-spinning-top’ idea proved popular and was promoted by other authors (e.g. Morris 1856; Thomson 1923). Later, others questioned the ability of guillemot eggs to rotate on its axis (e.g. MacGillivray 1852; Seebohm 1885; Wade 1903; also reviewed in Birkhead 2016; Birkhead & Thompson 2019). In particular, Wade (1903) highlighted that Common Guillemot eggs would require unreasonable force to actually behave in a spinning top like motion, and Birkhead (2016, 2017) has suggested that Hewitson’s (1831) hypothesis was an artefact of examining empty museum guillemot eggs that behave entirely different to an intact egg. Specifically, intact eggs with their internal fluid contents have significantly different masses and centre of gravity that prevents movement similar to a spinning top (Birkhead 2016, 2017).

More recently, another popular adaptative explanation for the pyriform-shaped guillemot egg is ‘rolling-in-an-arc’, first suggested by Belopol’skii (1961). This hypothesis proposed that the pyriform shape allows for an egg to roll in an arc, should it be disturbed, and thus reduce the risk of it rolling off the breeding ledge. A number of studies have observed that Common Guillemot eggs do roll in an arc and that this arc seems to be typically tighter than that of the egg of another close relative, the Razorbill *Alca torda*, whose eggs are considerably less pyriform (Belopol’skii 1961; Ingold 1980). Tschanz et al.’s (1969) experimental tests on model eggs demonstrated that more pyriform-shaped eggs roll in a tighter arc and, therefore, have augmented protection from rolling off breeding ledges. However, this result was based on plaster eggs and subsequently did not hold when real Common Guillemot and Razorbill eggs were tested on natural substrates (Ingold 1980). Most recently, Hays and Hauber (2018) re-examined the rolling-in-an-arc hypothesis and found evidence to suggest that certain shape traits associated with the pyriform egg form can suppress displacement, thus providing additional support to the adaptive explanation. Hays and Hauber (2018) improved on the previous studies by Tschanz et al. (1969) and Ingold (1980) by utilising quantified measures of both egg shape and egg arc displacement traits, that were absent in the earlier studies. However, Hays and Hauber (2018) also used model eggs and on surfaces that did not necessarily represent natural substrates observed at typical guillemot breeding sites, which hence necessitates some caution over the results. This caution over Hays and Hauber’s (2018) results is necessary considering apparent differences between rolling results of model and real eggs tested either on artificially flat and smooth surfaces or actual breeding cliff ledges in previous studies (Tschanz et al. 1969; Ingold 1980).

Whilst some evidence exists for the rolling-in-an-arc hypothesis, there are a number of reasons why this explanation for the Common Guillemot's pyriform egg is unlikely. First, described arc distances of rolling guillemot eggs are often wider than the ledges on which Common Guillemots breed (see Harris & Birkhead 1985; Birkhead & Nettleship 1987). Hays and Hauber (2018), for instance, noted in their rolling experiments on a 1 metre wide slope, that over 75% of model eggs were 'lost' (i.e. the model eggs rolled beyond the trackable length of 1 metre) at a slope angles of 8, 10 and 15 degrees. Many Common Guillemots, in fact, breed at slope angles steeper than 15 degrees (Birkhead et al. 2018), and often on ledges narrower than 1 metre (J.E. Thompson & T.R. Birkhead, *per. obs.*). Hence, it is difficult to observe how selection for pyriform-shaped eggs based on rolling arc characteristics would prove strong, especially considering that apparent benefits of reduced egg displacement/loss entirely erode at slope angles that can often be seen at Common Guillemot breeding cliff ledges (Hays & Hauber 2018). Second, during incubation, Common Guillemots typically incubate facing up-slope towards the cliff face with the 'pointed' end of the egg facing outwards towards the cliff edge. Hence, if disturbed, guillemot eggs would roll *outwards* towards the cliff edge and thus presumably increase the risk of egg loss (Birkhead et al. 2017b). Third, previous authors have highlighted that Brünnich's Guillemots appear to have less pyriform eggs than Common Guillemots (Belopol'skii 1961; Harris & Birkhead 1985; but see Hays & Hauber 2018), despite typically breeding on narrower cliff ledges (Birkhead & Nettleship 1987). This appears contradictory to what we might expect considering the rolling-in-an-arc hypothesis (but see Hays & Hauber 2018), and has been previously acknowledged as such by Ingold (1980). However, Ingold (1980) attempted to explain this apparent anomaly by highlighting a possible interaction between egg shape and mass on rolling trajectories. Specifically, he suggested that Brünnich's Guillemot eggs are typically lighter in mass than Common Guillemot eggs and, therefore, would result in them rolling in a smaller, tighter arc, thus making them less vulnerable to rolling off the cliff edge compared to Common Guillemot eggs. However, Ingold (1980) provided no evidence to support this assertion.

Clearly, much uncertainty has surrounded the question as to the point of the 'pointed' end of a Common Guillemot egg. Part of this uncertainty was linked to the lack of any methods to accurately quantify egg shapes like that of the Common Guillemot's pyriform egg. With Biggins et al.'s (2018) method, we were in a better position to explore the various adaptive explanations for the pyriform guillemot egg and we have published several papers on this topic (Birkhead et al. 2017a, 2017b, 2018; Jackson et al. 2018; also see section 1.3. for further information).

1.3. Thesis layout

The main aim of the papers presented here was to contribute to our further understanding of the potential evolutionary drivers and functions of the variation of avian egg form observed across birds. To address these questions, it was necessary to develop a robust method of acquiring accurate, quantifiable measures of egg shape traits, which integrates previously underused mathematical modelling methods presented by Preston (1953) that has been shown to adequately capture all forms of egg shape variation. **Chapter 2** presents Biggins et al. (2018), which introduces both a novel method for photographing eggs and a readily available automated image processing script, based on Preston's (1953) mathematical modelling, and produces three, interpretable shape indices (*pointedness*, *elongation* and *polar asymmetry*; see **Chapter 2** for definitions). The study also examines the accuracy of this method compared with other modelling methods (Carter 1968; Carter & Morley Jones 1970; Baker 2002; Troscianko 2014). The method presented in **Chapter 2** underpins all of the subsequent published quantitative work presented in this thesis.

Considering the unique pyriform egg shape produced by Common Guillemots (Tschanz et al. 1969; Birkhead 1993; Stoddard et al. 2017), and the limited evidence for any previously proposed adaptive explanations for this shape (see Birkhead 2016, 2017), our initial research focussed on the potential evolutionary drivers and functions of egg shape in this species. Furthermore, given that Common Guillemot egg shape is somewhat of an outlier to many other egg shapes exhibited by birds (Birkhead 2016; Stoddard et al. 2017), studying this extreme shape might provide insights into unique adaptive strategies that are potentially masked at higher taxonomic levels (Hall 2011; see Stoddard et al. 2017), and justifies focused research on such extreme properties (Barnett and Lewis 1994; Hays & Hauber 2018).

Chapter 3 comprises an account of the life and work of Edward Walter Wade (Birkhead & Thompson 2019). Wade was a regular collector of Common Guillemot eggs at Bempton Cliffs on the North Yorkshire coast, an area that was known for annual Common Guillemot egg harvests by local farm labourers known locally as the 'climmers', until the collecting of wild birds' eggs was made illegal in

1954 (Nelson 1907; Vaughan 1998; Birkhead 2016). The number of eggs collected during these annual harvests have been estimated to be anywhere from a few thousand to over a hundred thousand; estimates from the 1920-30's place the annual harvest at 48,000 (Birkhead 2016). Eggs collected by the climmers went on to be sold for food consumption and often to egg collectors, and many museum egg collections contain guillemot eggs harvested from Bempton Cliffs (Birkhead 2016). Because Wade was a climber (but not a 'climmer') himself, he – unlike most other collectors – had many opportunities for direct interactions with breeding Common Guillemots and their eggs. We examine in the paper how his observations led him to question the validity of the previously proposed 'spin-like-a-spinning-top' hypothesis (Hewitson 1831; Morris 1856; Thomson 1923) for the adaptation function of pyriform guillemot eggs. Furthermore, we place Wade's contributions into the wider context of the research field exploring the adaptive functions of Common Guillemot egg shape and highlight the importance of direct observations and experiences of breeding ledges when attempting to make biological meaningful adaptive hypotheses.

Given the conflicting evidence for the rolling-in-an-arc hypothesis (Belopol'skii 1961; Tschanz et al. 1965; Ingold 1980), **Chapter 4** presents a published paper by Birkhead et al. (2017a) that seeks to re-examine the plausibility of this hypothesis. Specifically, our study assesses the relationship between 'pointedness' shape index (Biggins et al. 2018) and egg volume to examine the validity of Ingold's (1980) proposed shape-mass interaction hypothesis for explaining contradictory results and apparent biological anomalies (see above section 1.2.3. for further details). Through the examination of such interactions in both Brünnich's and Common Guillemot eggs, we assess the validity of Ingold's (1980) hypothesis and, consequently, the plausibility of the rolling-in-an-arc hypothesis.

Because of the limited evidence for the rolling-in-an-arc hypothesis, we developed alternative hypotheses for the adaptive function of the pyriform egg in Common Guillemots. **Chapter 5** presents a paper by Birkhead et al. (2017b) that proposes two alternative adaptive hypotheses relating to: (i) the prevention and/or limitation of mechanical damage, and (ii) minimising the consequences of eggshell faecal/debris contamination. These hypotheses were considered based on observations that Common Guillemots typically breed at high densities (Birkhead 1977, 1993) and indiscriminately defecate, resulting in breeding ledges being covered in guano (Tschanz 1990; Birkhead 2016). For the faecal/debris contamination hypothesis, the study presents quantifiable measurements of eggshell porosity and the extent of faecal contamination between eggs of Common Guillemots and Razorbills (the latter that breed less densely and have much cleaner breeding sites, Bédard 1969; J.E. Thompson & T.R. Birkhead, *per. obs.*), that provides initial support for this proposed hypothesis.

Previously, it has been suggested by a research group led by Dr. Steven Portugal that the Common Guillemot's eggshell surface microstructures provide self-cleaning properties (reported online at: https://phys.org/news/2013-07-unique-shell-guillemot-eggs-edge.html). Yet, despite the wide media coverage, they provided no published evidence to support this claim (Jackson et al. 2018). Hence, **Chapter 6** presents a paper by Jackson et al. 2018 that tests the validity of the self-cleaning properties of Common Guillemot eggshell surfaces. In part of this follow up study by Jackson et al. 2018, novel experimental techniques were utilised to examine the potential negative impacts of faecal/debris contamination on eggshell surfaces on gas conductance. Indeed, other studies have shown that faecal contamination of an eggshells can result in a reduction in gas exchange, and the facilitation of microbial infections, both of which can result in embryo mortality (Board 1982, Verbeek 1984). Hence, assessing whether contamination of Common Guillemot eggshells by faecal and debris matter, specific to their breeding environment, does unequivocally reduce gas conductance is necessary to further support the plausibility of the proposed faecal/debris contamination hypothesis.

Chapter 7 comprises a study (by Birkhead et al. 2018) that proposes that the Common Guillemot's pyriform egg provides greater stability on the natural substrate of the breeding site, and thus mitigates egg displacement/rolling in the first place. The study tests this novel hypothesis by assessing the stability of real, intact Common Guillemot and Razorbill eggs with quantified shape using two unique experimental set-ups.

Since studies conducted at different taxonomic levels can identify different significant adaptive selection and/or anatomical constraints evolutionary trends for avian egg shape variation (e.g. Andersson 1978; Barta & Székely 1997; Birkhead et al. 2017b, 2018; Stoddard et al. 2017; Duursma et al. 2018; Hays & Hauber 2018; also see Hall 2011), we looked to examine potential evolutionary drivers of egg shape at a higher taxonomic level than our previous studies. **Chapter 8** comprises of work by Birkhead et al. (2019) that tests whether incubation behaviours and characteristics drives selection for specific egg shapes in alcids (Alcidae) and penguins (Spheniscidae), two taxa that exhibit considerable variation in egg shape and incubation environment and behaviour (Nettleship & Birkhead

1985; Williams 1995; Gaston & Jones 1998; Stoddard et al. 2017; Birkhead et al. 2019; del Hoyo et al. 2020).

Finally, **Chapter 9** summarises the main research findings of the published papers and discusses these in the context of the wider literature. I emphasise the insights our studies have contributed and finish by highlighting what future directions of research might be necessary to continue to improve our understanding of the evolutionary drivers and function of avian egg shape variation.

In the **Appendices**, I also present three other papers (one in preparation and the other two in press to be published) that highlight additional research I have worked on. These papers demonstrate additional applications of the method developed in **Chapter 2**, in addition to a couple of them using and building on from findings/discussions presented in the main chapters of this thesis.

1.4. Acknowledgement of collaborative work within the thesis

The candidate confirms that the work submitted is their own, except where work has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated at the start of each data chapter. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

References in Chapter 1:

Andersson, M. (1978). Optimal egg shape in waders. *Ornis Fennica*, **55**, 105-109.

Anten-Houston, M. V., Ruta, M. and Deeming, D. C. (2017). Effects of phylongeny and locomotor style on the allometry of body mass and pelvic dimensions in birds. *Journal of Anatomy*, **231**, 342-358.

Ar, A., Paganelli, C. V., Reeves, R. B., Greene, D. G. and Rahn, H. (1974). The Avian Egg: Water Vapor Conductance, Shell Thickness, and Functional Pore Area. *The Condor*, **76**, 153-158.

Ar, A. and Rahn, H. (1985). Pores in Avian Eggshells: Gas Conductance, Gas Exchange and Embryonic Growth Rate. *Respiration Physiology*, **61**, 1-20.

Ar, A., Rahn, H. and Paganelli, C. V. (1979). The Avian Egg: Mass and Strength. *The Condor*, **81**, 331-337.

Ar, A. and Yom-Tov, Y. (1978). The Evolution of Parental Care in Birds. *Evolution*, **32**, 655-669.

Arad, Z., Gavrieli-Levin, I. and Marder, J. (1988). Adaptation of the Pigeon Egg to Incubation in Dry Hot Environments. *Physiological Zoology*, **61**, 293-300.

Attard, M. R. G., Medina, I., Langmore, N. E., and Sherratt, E. (2017). Egg shape mimicry in parasitic cuckoos. *Journal of Evolutionary Biology*, **30**, 2079-2084.

Attard, M. R. G., Sherratt, E., McDonald, P., Young, I., Vidal-García, M. and Wroe, S. (2018). A new, three-dimensional geometric morphometric approach to assess egg shape. *PeerJ*, **6**, e5052.

Bain, M. M. (1991). A reinterpretation of eggshell strength. In: *Egg and Eggshell Quality.* (ed. Solomon, S. E.). Wolfe Publishing Limited: London. pp. 131-145.

Baker, D. E. (2002). A Geometric Method for Determining Shape of Bird Eggs. *The Auk*, **119**, 1179-1186.

Bán, M., Barta, Z., Muñoz, A. R., Takasu, F., Nakamura, H. and Moskát, C. (2011). The analysis of common cuckoo's egg shape in relation to its hosts' in two geographically distant areas. *Journal of Zoology*, **284**, 77-83.

Barnett, V. and Lewis, T. (1994). *Outliers in Statistical Data, Volume 3.* Wiley: New York.

Barta, Z. and Székely, T. (1997). The optimal shape of avian eggs. *Functional Ecology*, **11**, 656-662.

Bédard, J. (1969). Histoire naturelle du Gode, *Alca torda*, L., dans le golfe Saint-Laurent, province de Québec, Canada. *Étude du Service Canadien de la Faune – No. 7.*

Belopol'skii, L. O. (1961). *Ecology of Sea Colony Birds of the Barents Sea.* (translated from original 1957 publication by Ettinger R. and Salzmann C.). Israel Program for Scientific Translations: Jerusalem.

Biggins, J. D., Thompson, J. E. and Birkhead, T. R. (2018). Accurately quantifying the shape of birds' eggs. *Ecology and Evolution*, **8**, 9728-9738.

Birchard, G. F. and Deeming, D. C. (2009). Avian eggshell thickness: scaling and maximum body mass in birds. *Journal of Zoology*, **279**, 95-101.

Birkhead, T. R. (1977). The Effect of Habitat and Density on Breeding Success in the Common Guillemot (*Uria aalge*). *Journal of Animal Ecology*, **46**, 751-764.

Birkhead, T. R. (1993). *Great Auk Islands: A Field Biologist in the Arctic.* Poyser: London.

Birkhead, T. R. (2016). *The Most Perfect Thing: The Inside (and Outside) of a Bird's Egg.* Bloomsbury: London.

Birkhead, T. R. (2017). Vulgar errors: the point of a Guillemot's egg, or why the widely believed explanation for the guillemot's pointed egg is almost certainly wrong. *British Birds*, **110**, 456-467.

Birkhead, T. R. and Montgomerie, R. (2018). Rare red eggs of the Common Guillemot (*Uria aalge*): birds, biology and people at Bempton, Yorkshire, in the early 1900s. *Archives of Natural History*, **45**, 69-79.

Birkhead, T. R. and Nettleship, D. N. (1987). Ecological relationships between Common Murres, *Uria aalge* and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. II: breeding success and site characteristics. *Canadian Journal of Zoology*, **65**, 1630-1637.

Birkhead, T. R., Thompson, J. E. and Biggins, J. D. (2017a). Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: not a rolling matter? *Journal of Ornithology*, **158**, 679-685.

Birkhead, T. R., Thompson, J. E., Jackson, D. and Biggins, J. D. (2017b). The point of a Guillemot's egg. *Ibis*, **159**, 255-265.

Birkhead, T. R., Thompson, J. E. and Montgomerie, R. (2018). The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *The Auk*, **135**, 1020-1032.

Birkhead, T. R., Thompson, J. E., Biggins, J. D. and Montgomerie, R. (2019). The evolution of egg shape in birds: selection during the incubation period. *Ibis*, **161**, 605-618.

Birkhead, T. R. and Thompson, J. E. (2019). Wade's Birds of Bempton Cliffs and his observations on Guillemot (*Uria aalge*) eggs. *Archives of Natural History*, **46**, 240-252.

Board, R. G. (1982). Properties of Avian Egg Shells and their Adaptive Value. *Biological Reviews*, **57**, 1-28.

Board, R. G. and Fuller R. (1974). Non-Specific Antimicrobial Defence of the Avian Egg, Embryo and Neonate. *Biological Reviews*, **49**, 15-49.

Board, R. G. and Halls, N. A. (1973a). The cuticle: a barrier to liquid and particle penetration of the shell of the hen's egg. *British Poultry Science*, **14**, 69-97.

Board, R. G. and Halls, N. A. (1973b). Water uptake by eggs of mallards and guinea fowl. *British Poultry Science*, **14**, 311-314.

Board, R. G. and Scott, V. D. (1980). Porosity of the Avian Eggshell. *American Zoologist*, **20**, 339-349.

Board, R. G., Tullett, S. G. and Perrott, H. R. (1977). An arbitrary classification of the pore systems in avian eggshells. *Journal of Zoology*, **182**, 251-265.

Carey, C., Rahn, H. and Parisi, P. (1980). Calories, Water, Lipid and Yolk in Avian Eggs. *The Condor*, **82**, 335-343.

Carter, T. C. (1968). The hen's egg: A mathematical model with three parameters. *British Poultry Science*, **9**, 165-171.

Carter, T. C. and Morley Jones, R. (1970). The hen's egg: Shell shape and size parameters and their interrelations. *British Poultry Science*, **11**, 179-188.

Cassey, P., Portugal, S. J., Maurer, G., Ewen, J. G., Boulton, R. L., Hauber, M. E. and Blackburn, T. M. (2010). Variability in Avian Eggshell Colour: A Comparative Study of Museum Eggshells. *PLoS ONE*, **5**, e12054.

Cherry, M. I. and Gosler, A. G. (2010). Avian eggshell coloration: new perspectives on adaptive explanations. *Biological Journal of the Linnean Society*, **100**, 753-762.

Claramunt, S., Derryberry, E. P., Remsen, J. V. and Brumfield, R. T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1567-1574.

D'Alba, L., Jones, D. N., Badawy, H. T., Eliason, C. M. and Shawkey, M. D. (2014). Antimicrobial properties of a nanostructured eggshell from a compost-nesting bird. *Journal of Experimental Biology*, **217**, 1116-1121.

D’Alba, L., Maia, R., Hauber, M. E. and Shawkey, M. D. (2016). The evolution of eggshell cuticle in relation to nesting ecology. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160687.

D’Alba, L., Torres, R., Waterhouse, G. I. N., Eliason, C., Hauber, M. E. and Shawkey, M. D. (2017). What Does the Eggshell Cuticle Do? A Functional Comparison of Avian Eggshell Cuticles. *Physiological and Biochemical Zoology*, **90**, 588-599.

Deeming, D. C. (1987). Effect of cuticle removal on the water vapour conductance of egg shells of several species of domestic bird. *British Poultry Science*, **28**, 231-237.

Deeming, D. C., ed. (2002). Avian Incubation: Behaviour, Environment and Evolution. Oxford University Press: Oxford.

Deeming, D. C. (2007a). Effects of phylogeny and hatchling maturity on allometric relationships between female body mass and the mass and composition of bird eggs. *Avian and Poultry Biology Reviews*, **18**, 21-37.

Deeming, D. C. (2007b). Allometry of mass and composition in bird eggs: effects of phylogeny and hatchling maturity. *Avian and Poultry Biology Reviews*, **18**, 71-86.

Deeming, D. C. (2018). Effect of composition on shape of bird eggs. *Journal of Avian Biology*, **49**, e01528.

Deeming, D. C. and Ruta, M. (2014). Egg shape changes at the theropod-bird transition, and a morphometric study of amniote eggs. *Royal Society Open Science*, **1**, 140311.

Deeming, D. C. and Mayr, G. (2018). Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their eggs. *Journal of Evolutionary Biology*, **31**, 701-709.

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. and de Juana, E., eds. (2020). *Handbook of the Birds of the World Alive*. Lynx Edicions: Barcelona. Available at: http://www.hbw.com/ (accessed 15 January 2020).

Duursma, D. E., Gallagher, R. V., Price, J. J. and Griffith, S. C. (2018). Variation in avian egg shape and nest structure is explained by climatic conditions. *Scientific Reports*, **8**, 4141.

Gaston, A. J. and Jones, I. L. (1998). *The Auks.* Oxford University Press: Oxford.

Gaston, A. J. and Nettleship, D. N. (1981). *The Thick-billed Murres of Prince Leopold Island.* Canadian Wildlife Service Monographs, No. 6: Ottawa.

Gole, V. C., Chousalkar, K. K., Roberts, J. R., Sexton, M., May, D., Tan, J. and Kiermeier, A. (2014a). Effect of egg washing and correlation between eggshell characteristics and egg penetration by various *Salmonella typhimurium* strains. *PLoS ONE*, **9**, e90987.

Gole, V. C., Roberts, J. R., Sexton, M., May, D., Kiermeier, A. and Chousalkar, K. K. (2014b). Effect of egg washing and correlation between cuticle and egg penetration by various *Salmonella* strains. *International Journal of Food Microbiology*, **182-183**, 18-25.

Gosler, A. G. (2006). Yet even more ways to dress eggs. *British Birds*, **99**, 338-353.

Graham, C. H., Storch, D. and Machac, A. (2018). Phylogenetic scale in ecology and evolution. *Global Ecology and Biogeography*, **27**, 175-187.

Hall, B. K. (2011). *Evolution: Principles and Processes.* Jones and Bartlett Learning: Burlington.

Harris, M. P. and Birkhead, T. R. (1985). Breeding ecology of the Atlantic Alcidae. In: *The Atlantic Alcidae.* (eds. Nettleship, D. N. and Birkhead, T. R.). Academic Press: London. pp. 155-205.

Hauber, M. E., Bond, A. L., Kouwenberg, A-L., Robertson, G. J., Hansen, E. S., Holford, M., Dainson, M., Luro, A. and Dale, J. (2019). The chemical basis of a signal of individual identity: shell pigment concentrations track the unique appearance of Common Murre eggs. *Journal of the Royal Society Interface*, **16**, 20190115.

Hays, I. R. and Hauber, M. E. (2018). How the egg rolls: a morphological analysis of avian egg shape in the context of displacement dynamics. *Journal of Experimental Biology*, **221**, jeb178988.

Hewitson, W. C. (1831). *British oology: being illustrations of the eggs of British birds, with figures of each species, as far as practicable, drawn and coloured from nature: accompanied by descriptions of the materials and situation of their nests, number of eggs.* Empson: Newcastle upon Tyne.

Higginson, T. W. (1862). The life of birds. *Atlantic Monthly*, **10**, 368-376.

Hoyt, D. F. (1976). The Effect of Shape on the Surface-Volume Relationships of Birds' Eggs. *The Condor*, **78**, 343-349.

Ingold, P. (1980). Anpassungen der Eier und des Brutverhaltens von Trottellummen (*Uria aalge aalge* Pont.) an das Brüten auf Felssimsen. *Zeitschrift für Tierpsychologie*, **53**, 341-388.

Ishikawa, S-I., Suzuki, K., Fukuda, E., Arihara, K., Yamamoto, Y., Mukai, T. and Itoh, M. (2010). Photodynamic antimicrobial activity of avian eggshell pigments. *FEBS Letters*, **584**, 770-774.

Iverson, J. B. and Ewert, M. A. (1991). Physical characteristics of reptilian eggs and a comparison with avian eggs. In: *Egg Incubation: Its effects on embryonic development in birds and reptiles.* (eds. Deeming, D. C. and Ferguson, M. W. J.). Cambridge University Press: Cambridge. pp. 87-100.

Jackson, D., Thompson, J. E., Hemmings, N. and Birkhead, T. R. (2018). Common guillemot (*Uria aalge*) eggs are not self-cleaning. *Journal of Experimental Biology*, **221**, jeb188466.

Juang, J-Y., Chen, P-Y., Yang, D-C., Wu, S-P., Yen, A. and Hsieh, H-I. (2017). The avian egg exhibits general allometric invariances in mechanical design. *Scientific Reports*, **7**, 14205.

Kennedy, J. D., Borregaard, M. K., Jønsson, K. A., Marki, P. Z., Fjeldså, J. and Rahbek, C. (2016). The influence of wing morphology upon the dispersal, geographical distributions and diversification of the Corvides (Aves; Passeriformes). *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20161922.

Kilner, R. M. (2006). The evolution of egg colour and patterning in birds. *Biological Reviews*, **81**, 383-406.

Kipp, F. A. (1959). Der Handflügel-Index als flugbiologisches Maß. *Die Vogelwarte*, **20**, 77-86.

Köller, J. (2020). Egg Curves and Ovals. *Mathematische Basteleien*. Available at: http://www.mathematische-basteleien.de/eggcurves.htm (accessed on 16th January 2020).

Lack, D. (1958). The Significance of the colour of Turdine eggs. *Ibis*, **100**, 145-166.

Lahti, D. C. and Ardia, D. R. (2016). Shedding Light on Bird Egg Color: Pigment as Parasol and the Dark Car Effect. *The American Naturalist*, **187**, 547-563.

Lang, M. R. and Wells, J. W. (1987). A Review of eggshell pigmentation. *World's Poultry Science Journal*, **43**, 238-246.

Lockwood, R., Swaddle, J. P. and Rayner, J. M. V. (1998). Avian Wingtip Shape Reconsidered: Wingtip Shape Indices and Morphological Adaptations to Migration. *Journal of Avian Biology*, **29**, 273-292.

MacGillivray, W. (1852). *A History of British Birds, Indigenous and Migratory (Vol. V).* William S. Orr and Co.: London.

Mallock, A. (1925). The Shapes of Birds' Eggs. *Nature*, **116**, 312-313.

Mänd, R., Nigul, A. and Sein, E. (1986). Oomorphology: A New Method. *The Auk*, **103**, 613-617.

Mao, K-M., Murakami, A., Iwasawa, A. and Yoshizaki, N. (2007). The asymmetry of avian egg-shape: an adaptation for reproduction on dry land. *Journal of Anatomy*, **210**, 741-748.

Maurer, G., Portugal, S. J., Hauber, M. E., Mikšík, Russell, D. G. D. and Cassey, P. (2015). First light for avian embryos: eggshell thickness and pigmentation mediate variation in development and UV exposure in wild bird eggs. *Functional Ecology*, **29**, 209-218.

Mikhailov, K. E. (1997). *Avian Eggshells: An Atlas of Scanning Electron Micrographs.* BOC Occasional Publications No. 3. British Ornithologists' Club: Tring.

Mityay, I., Matsyura, A. and Jankowski, K. (2015). Application of Bird Egg Morphometrics in Phylogeny. *Acta Biologica Sibirica*, **1**(3-4), 92-102.

Montevecchi, W. A. (1976). Field Experiments on the Adaptive Significance of Avian Eggshell Pigmentation. *Behaviour*, **58**, 26-39.

Mónus, F. and Barta, Z. (2005). Repeatability Analysis of Egg Shape in a Wild Tree Sparrow (*Passer montanus*) Population: A Sensitive Method for Egg Shape Description. *Acta Zoologica Academiae Scientiarum Hungaricae*, **51**, 151-162.

Moreno, J. and Osorno, J. L. (2003). Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? *Ecology Letters*, **6**, 803-806.

Morris, F. O. (1856). *A History of British Birds.* Groombridge: London.

Mytiai, I. S. and Matsyura, A. V. (2019). Mathematical interpretation of artificial ovoids and avian egg shapes (part I). *Regulatory Mechanisms in Biosystems*, **10**, 92-102.

Mytiai, I. S., Shatkovska, O. V. and Ghazali, M. (2017). Size and shape of eggs of Neognathae: effects of developmental mode and phylogeny. *Canadian Journal of Zoology*, **95**, 359-366.

Nelson, T. H. (1907). *The Birds of Yorkshire.* A. Brown and Sons: London.

Nettleship, D. N. and Birkhead, T. R., eds. (1985). *The Atlantic Alcidae.* Academic Press: London.

Newton, A. V. (1896). *A dictionary of birds.* A and C Black: London.

Pennant, T. (1768). *British Zoology.* Benjamin White: London.

Pigot, A. and Tobias, J. A. (2015). Dispersal and the transition to sympatry in vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20141929.

Preston, F. W. (1953). The Shapes of Birds' Eggs. *The Auk*, **70**, 160-182.

Preston, F. W. (1968). The Shapes of Birds' Eggs: Mathematical Aspects. *The Auk*, **85**, 454-463.

Preston, F. W. (1969). Shapes of Birds' Eggs: Extant North American Families. *The Auk*, **86**, 246-264.

Rahn, H. and Ar, A. (1974). The Avian Egg: Incubation Time and Water Loss. *The Condor*, **76**, 147-152.

Rahn, H., Curran-Everett, L. and Booth, D. T. (1988). Eggshell Differences between Parasitic and Nonparasitic Icteridae. *The Condor*, **90**, 962-964.

Rahn, H. and Paganelli, C. V. (1989). Shell mass, thickness and density of avian eggs derived from the tables of Schönwetter. *Journal für Ornithologie*, **130**, 59-68.

Reisz, R. R. and Müller, J. (2004). Molecular timescales and the fossil record: a paleontological perspective. *Trends in Genetics*, **20**, 237-241.

Rensch, B. (1947). *Neuere Probleme der Abstammungslehre.* Ferdinand Enke: Stuttgart.

Ricklefs, R. E. (1977). Composition of Eggs of Several Bird Species. *The Auk*, **94**, 350-356.

Ricklefs, R. E. and Starck, J. M. (1998). Embryonic Growth and Development. In: *Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum.* (eds. Starck, J. M. and Ricklefs, R. E.). Oxford University Press: Oxford. pp. 31-58.

Romanoff, A. L. and Romanoff, A. J. (1949). *The Avian Egg.* John Wiley & Sons, Inc.: New York.

Saino, N., Martinelli, R., Biard, C., Gil, D., Spottiswoode, C. N., Rubolini, D., Surai, P. F. and Møller, A. P. (2007). Maternal immune factors and the evolution of secondary sexual characters. *Behavioral Ecology*, **18**, 513-520.

Samiullah, S. and Roberts, J. R. (2014). The eggshell cuticle of the laying hen. *World's Poultry Science Journal*, **70**, 693-708.

Sander, P. M. (2012). Reproduction in Early Amniotes. *Science*, **337**, 806-808.

Schönwetter, M. (1960-1992). *Handbuch der Oologie*. Akademie Verlag: Berlin.

Seebohm, H. (1885). *A History of British Birds, with Coloured Illustrations of their Eggs. Volume 3.* R. H. Porter, and Dulau and Co.: London.

Shatkovska, O. V., Ghazali, M., Mytiai, I. S. and Druz, N. (2018). Size and shape correlation of birds' pelvis and egg: Impact of developmental mode, habitat, and phylogeny. *Journal of Morphology*, **279**, 1590-1602.

Shawkey, M. D., Kosciuch, K. L., Liu, M., Rohwer, F. C., Loos, E. R., Wang, J. M. and Beissinger, S. R. Do birds differentially distribute antimicrobial proteins within clutches of eggs? *Behavioral Ecology*, **19**, 920-927.

Smart, I. H. M. (1991). Egg shape in birds. In: In: *Egg Incubation: Its effects on embryonic development in birds and reptiles.* (eds. Deeming, D. C. and Ferguson, M. W. J.). Cambridge University Press: Cambridge. pp. 101-116.

Smith, N. G. (1966). Adaptations to cliff-nesting in some Arctic gulls (Larus). *Ibis*, **108**, 68-83.

Soler, J. J., Moreno, J., Avilés, J. M. and Møller, A. P. (2005). Blue and green egg-color intensity is associated with parental effort and mating system in passerines: support for the sexual selection hypothesis. *Evolution*, **59**, 636-644.

Solomon, S. E. (1987). Egg shell pigmentation. In: *Egg quality – current problems and recent advances* (eds. Wells, R. G. and Belyarin, C. G.). Butterworths: London. pp. 147-157.

Sotherland, P. R. and Rahn, H. (1987). On the Composition of Bird Eggs. *The Condor*, **89**, 48-65.

Sparks, N. H. C. and Board, R. G. (1984). Cuticle, shell porosity and water uptake through hens' eggshells. *British Poultry Science*, **25**, 267-276.

Spottiswoode, C. N. and Stevens, M. (2010). Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proceeding of the National Academy of Sciences of the United States of America*, **107**, 8672-8676.

Stein, L. R. and Badyaev, A. V. (2011). Evolution of eggshell structure during rapid range expansion in a passerine bird. *Functional Ecology*, **25**, 1215-1222.

Stevens, M. (2011). Avian vision and egg colouration: concepts and measurements. *Avian Biology Research*, **4**, 168-184.

Stoddard, M. C., Sheard, C., Akkaynak, D., Yong, E. H., Mahadevan, L. and Tobias, J. A. (2019). Evolution of avian egg shape: underlying mechanisms and the importance of taxonomic scale. *Ibis*, **161**, 922-925.

Stoddard, M. C. and Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1387-1393.

Stoddard, M. C., Yong, E. H., Akkaynak, D., Sheard, C., Tobias, J. A. and Mahadevan, L. (2017). Avian egg shape: Form, function and evolution. *Science*, **356**, 1249-1254.

Sumida, S. S. and Martin, K. L. M., eds. (1997). *Amniote Origins: Completing the Transition to Land*. Academic Press: London.

Swynnerton, C. F. M. (1916). On the Coloration of the Mouths and Eggs of Birds. – II. On the Coloration of Eggs. *Ibis*, **4**, 529-606.

Tarchanoff, I. R. (1884). Über die Verschiedenheiten des Eiwesizes bei gefiredert geborenen (Nestflüchter) und bei nakt geborenen (Nesthocker) Vögeln und über die Verhältnisse zwischen dem Dotter und dem Eiereiweiss. (Biologisch-chemishe Untersuchung). *Pflügers Archiv - European Journal of Physiology*, **33**, 303-378.

Thompson, D'A. W. (1917). *On Growth and Form.* Cambridge University Press: Cambridge.

Thompson, M. B. and Goldie, K. N. (1990). Conductance and structure of eggs of Adelie penguins, *Pygoscelis adeliae*, and its implications for incubation. *The Condor*, **92**, 304-312.

Thomson, A. L. (1964). *A New Dictionary of Birds.* Nelson: London.

Thomson, J. A. (1923). *The Biology of Birds.* Macmillan: New York.

Todd, P. H. and Smart, I. H. M. (1984). The shape of birds' eggs. *Journal of Theoretical Biology*, **106**, 239-243.

Troscianko, J. (2014). A simple tool for calculating egg shape, volume and surface area from digital images. *Ibis*, **156**, 874-878.

Tschanz, B. (1959). Zur Brutbiologie der Trottellume (*Uria aalge aalge* Pont.). *Behaviour*, **14**, 1-100.

Tschanz, B. (1990). Adaptations for breeding in Atlantic alcids. *Netherlands Journal of Zoology*, **40**, 688-710.

Tschanz, B., Ingold, P. and Lengacher, H. (1969). Eiform und Bruterfolg bei Trottellummen (*Uria aalge*). *Ornithologische Beobachter*, **66**, 25-42.

Tullett, S. G. and Board, R. G. (1977). Determinants of avian eggshell porosity. *Journal of Zoology*, **183**, 203-211.

Tyler, C. (1969). Avian Egg Shells: Their Structure and Characteristics. *International Review of General and Experimental Zoology*, **4**, 81-130.

Underwood, T. J. and Sealy, S. G. (2002). Adaptive significance of egg coloration. In: *Avian Incubation: Behaviour, Environment and Evolution* (ed. Deeming, D. C.). Oxford University Press: Oxford. pp. 280-298.

Vaughan, R. (1998). *Seabird City: A Guide to the Breeding Seabirds of the Flamborough Headland.* Smith Settle: Otley.

Verbeek, N. A. M. (1984). The effects of adult fecal material on egg hatchability in Glaucous-winged Gulls (*Larus glaucescens*). *The Auk*, **101**, 824-829.

Vleck, C. M. and Vleck, D. (1987). Metabolism and Energetics of Avian Embryos. *The Journal of Experimental Zoology Supplement*, **1**, 111-125.

Wade, E. W. (1903). The Birds of Bempton Cliffs. *Transactions of the Hull Scientific and Field Naturalists' Club*, **3**, 1-26.

Wallace, A. R. (1889). *Darwinism: An exposition of the theory of natural selection with some of its applications.* Macmillan and Co.: London.

Walters, M. (1994). *Birds' Eggs.* Dorling Kindersley: London.

Warham, J. (1990). *The Petrels: Their Ecology and Breeding Systems.* Academic Press: London.

Wellman-Labadie, O., Picman, J. and Hincke, M. T. (2008). Comparative antibacterial activity of avian egg white protein extracts. *British Poultry Science*, **49**, 125-132.

Williams, T. D. (1995). *The Penguins.* Oxford University Press: Oxford.

Wisocki, P. A., Kennelly, P., Rivera, I. R., Cassey, P., Burkey, M. L. and Hanley, D. (2020). The global distribution of avian eggshell colours suggest a thermoregulatory benefit of darker pigmentation. *Nature Ecology and Evolution*, **4**, 148-155.

CHAPTER 2:

Accurately quantifying the shape of birds’ eggs

Accurately quantifying the shape of birds’ eggs

Biggins, J. D., Thompson, J. E. and Birkhead, T. R. (2018). *Ecology and Evolution*, **8**, 9728-9738.

Original article and Supplementary Materials can be found using the link below:

https://onlinelibrary.wiley.com/doi/10.1002/ece3.4412

Chapter context and thesis author’s contributions: Previous studies of avian egg shape patterns have lacked a standardised method for quantifying egg shape that is both intuitive and able to accurately quantify the shapes of *all* egg shapes. This chapter presents a paper in Ecology and Evolution in which we introduce a novel automated 2D-image shape analysis modelling method that is able to accurately quantify all egg shapes.

My contribution to this published article comprised a novel method for photographing eggs and subsequently processing images before automated quantification of egg shape. Using this developed method, I have measured and photographed several thousand eggs of over 200 different bird species both in museum collections and within the field. All eggs in the field were photographed and measured under licences from Natural Resource Wales. I was responsible for the fine-tuning of photographic methods for obtaining egg silhouette images and the necessary calibrations of these images (e.g. performing lens distortion correction) to obtain suitable photos for accurate quantification of egg shape. I tested the importance of egg positioning within images and how this can affect the quantification of shape indices; for this, I analysed the consequences of incorrectly positioning eggs for photography that is included in the paper. I performed all the automated shape analysis script runs and provided the collated data, as well as feedback on the script’s effectiveness during development, to J.D. Biggins. I also contributed to discussions, along with my co-authors, on possible ways to measure certain aspects of shape and potential improvements to the automated script.

Co-authors' contributions: J.D. Biggins and T.R. Birkhead wrote the initial draft of the article. J.D. Biggins did the main research for the article, with some contributions from T.R. Birkhead. T.R. Birkhead assisted with the measurement of eggs. The mathematics and the automated script for 2D-image analyses were developed by J.D. Biggins. Analytical comparisons of different shape modelling methods presented in the published article were carried out by J.D. Biggins. J.D. Biggins and T.R. Birkhead also contributed to the development and improvement of novel shape analysis methods. T.R. Birkhead managed the overall project and conceived the initial idea to develop a new automated shape analysis method.

Received: 9 May 2018 | Revised: 21 June 2018 | Accepted: 26 June 2018
DOI: 10.1002/ece3.4412

ORIGINAL RESEARCH

WILEY Ecology and Evolution Open Access

Accurately quantifying the shape of birds' eggs

John D. Biggins[1] | **Jamie E. Thompson**[2] | **Tim R. Birkhead**[2]

[1]School of Mathematics and Statistics, The University of Sheffield, Sheffield, UK

[2]Department of Animal and Plant Sciences, The University of Sheffield, Sheffield, UK

Correspondence
John D. Biggins, School of Mathematics and Statistics, The University of Sheffield, Sheffield, UK.
Email: j.biggins@sheffield.ac.uk

Funding information
Leverhulme Trust

Abstract

Describing the range of avian egg shapes quantitatively has long been recognized as difficult. A variety of approaches has been adopted, some of which aim to capture the shape accurately and some to provide intelligible indices of shape. The objectives here are to show that a (four-parameter) method proposed by Preston (1953, *The Auk*, 70, 160) is the best option for quantifying egg shape, to provide and document an R program for applying this method to suitable photographs of eggs, to illustrate that intelligible shape indices can be derived from the summary this method provides, to review shape indices that have been proposed, and to report on the errors introduced using photographs of eggs at rest rather than horizontal.

KEYWORDS
asymmetry, elongation, guillemot, pointedness, pyriform, shape indices, shape parameters

1 | INTRODUCTION

Birds' eggs occur in a remarkable range of sizes and shapes, from almost spherical to extremely elongate and symmetrical to pointed at one end (pyriform). The causes and evolutionary consequences of interspecific differences in avian egg shape have puzzled biologists for over a century, yet the way different egg shapes are produced within the oviduct and the adaptive significance of egg shape remain largely unresolved. One reason for this has been the difficulty of quantifying egg shape, as no single index captures effectively the full range of avian egg shapes or, indeed, other taxa such as reptiles (Birkhead, Thompson, Jackson, & Biggins, 2017; Deeming & Ruta, 2014; Stoddard et al., 2017).

It is convenient to speak of the two pointed ends of the egg as poles, giving a natural sense to "latitude" (distance between the poles along the line joining them), "equator" (the points on the surface at equal distance from the two poles), and "meridian" (the profile of the surface from pole to pole). In an early study of avian egg shape, Mallock (1925) examined the implications of the observation that eggs have circular latitudinal cross-sections. It is this observation that justifies capturing egg shape through a suitable formula for the meridian and means that from this, together with a length measurement, any characteristic, such as volume or surface area, of the egg shape can be obtained. Thus, although the focus here is on avian egg shapes, the methods would apply also to eggs of other taxa that have circular cross-sections. Several authors (Mallock, 1925; Okabe, 1952; Stoddard et al., 2017; Thompson, 1942) have considered the mechanisms by which different egg shapes might be achieved. We have no additional insights into that topic, which is distinct from seeking a simple accurate summary for the shape.

Romanoff and Romanoff (1949, p88) state "the numerous variations in the contour of individual eggs obviously cannot be expressed in mathematical terms" and, commenting on Thompson's (1942) magnificent treatise "On Growth and Form", Preston (1953, p160) said that Thompson "seemed to throw up his hands in the belief that egg shape is indescribable, particularly if it happens to be a guillemot's (=murre's)" [i.e. *Uria aalge*]. Preston (1953) went on to propose an approach that captures the whole range of the shapes of eggs through four parameters. This insight underpins the subsequent studies by Preston (1968) and Todd and Smart (1984).

Although Preston (1953) solved the problem of capturing egg shape, the parameters he employed do not have a simple intuitive relation to the most striking aspects of shape. Thus, other, more direct, measurements have been proposed (see Section 2.6 below for further discussion). In particular, informed by his earlier insights, Preston (1968) identified three indices (which he calls asymmetry, bicone and elongation) that he considered captured the variation in avian egg shape, including the pyriform (pointed) eggs of birds such as the guillemot. However, this set of indices has not been widely adopted, for three reasons: (a) two of his indices (asymmetry and bicone) depend on a measure of the curvature at the ends of an egg that he obtained using a specially constructed device (a spherometer); (b) the two indices derived using the spherometer are, as Preston explains, motivated by, but are not the same as, other indices that are more directly related to the fitted shape but less practical to measure; (c) his mathematical formulations may have deterred some researchers from exploring his ideas (see also Mänd, Nigul, & Sein, 1986, p613).

Instead, researchers have often used just two simpler indices: (a) asymmetry – the extent to which the latitude with widest breadth deviates from the equator; (b) elongation – length relative to breadth. Neither of these is precisely specified by these descriptions and a number of variants exist (see Section 2.6 below). Thus, the potential for confusion is considerable: the same shape index is sometimes referred to by different names by different authors, and in some cases, different shape indices are referred to by the same name. In general, indices are not methods for capturing egg shape accurately in all cases, but, rather, are ways of obtaining certain summary measures that are intuitively related to key aspects of shape.

An important aspect of these different measures of "asymmetry" and "elongation" is that they all fail to deal satisfactorily with eggs of certain shapes, in particular pyriform eggs produced by some alcids and waders (shorebirds). For example, the recent wide-ranging comparative study by Stoddard et al. (2017) uses two indices, based on Baker's (2002) formulations. However, this method did not quantify the shape of pyriform eggs sufficiently accurately and so they were excluded from their analysis (see figure S2 in Stoddard et al., 2017).

Digital photography and the automated handling of the digital images mean that the field constraints that influenced Preston's (1968) choice of summary indices no longer apply. Now, instead, Preston's (1953) original ideas for summarizing egg shape can be applied automatically — a possibility he anticipated (Preston, 1969; p262–3). The software we have developed (see the Supporting Information: Supplementary Material,[1] Section SupM5), which works best with egg silhouettes, does this.

The studies by Barta and Székely (1997), Mónus and Barta (2005) and Bán et al. (2011) are already in this vein, working from photographs, except they did not process images automatically, and, presumably as a consequence, used a limited number of points on the meridian in the curve fitting. Mityay, Matsyura, and Jankowski (2015) do seem to have processed a large number of photographs and fitted Preston parameters, although these are, rather misleadingly, attributed to Frantsevich (2015) rather than Preston (1953). Moreover Mityay et al. (2015) give no detail of their fitting methods. Attard, Medina, Langmore, and Sherratt (2017) processed egg images automatically by drawing on sophisticated Fourier techniques designed to capture even very complicated closed contours, to produce a large set of coefficients and then reduced the coefficient set using principal components. However, egg profiles are really very simple closed contours, as the success of Preston's approach shows, which can be summarized much more directly.

Alternative methods of summarizing egg shape have been proposed by Carter (1968), Carter and Morley Jones (1970), Baker (2002) and Troscianko (2014). When compared with Preston's (1953) proposal, each of these is less effective in capturing egg shape for some eggs (see Sections 3.1 and 3.2 below). Several other possible mathematical forms have been identified, as the web pages maintained by Köller (2017) illustrate. In particular, Thompson (1942, p936) mentions the Cartesian Oval as a proposal going back to the middle of the nineteenth century, although he points out that this proposal "fails in such a case as the guillemot."

The aims here are to: (a) enable, via the accompanying software, the automated use of Preston's (1953) original proposal for capturing egg shape, and to extend it somewhat; (b) illustrate that that proposal has sufficient flexibility to capture very accurately the shape of all eggs including pyriform eggs and that the methods of Carter (1968), Carter and Morley Jones (1970), Baker (2002) and Troscianko (2014) are less effective; (c) show that egg positioning for the photographs matters; (d) illustrate that once Preston's parameter's and the length of the egg are available, any characteristic of the egg shape and size can be obtained – in particular, three interpretable indices of shape: Elongation, Pointedness, and Polar Asymmetry (described in Section 2.5); and (e) present a review of the various measures of egg shape that have been used previously and their relationships and demonstrate the appropriateness of the indices Elongation, Pointedness and Polar Asymmetry for describing the shape of pyriform eggs.

2 | METHODS

2.1 | Formulae for egg shape

Imagine an egg with its longest axis horizontal, on the x-axis, and with the length scale arranged so that the two poles are at −1 and 1, which means the egg's length is scaled to be two. The height of the egg outline above the horizontal axis at x is $y(x)$, and, because latitudinal cross-sections are circular, the lower half of the egg, below the horizontal axis, will be a mirror image. Various mathematical forms have been proposed for the meridian $y(x)$, with parameters that can be estimated in order to match the shape of a particular egg. A general strategy is to express $y(x)$ as a suitable modification of the equation for a circle: Preston (1953, Equation (4)) and Todd and Smart (1984, Equation (2)) proposed

$$y(x) = f(x)\sqrt{1 - x^2}. \tag{1}$$

Equation (4) in Preston (1953) looks different from Equation (1), but this is only because in his presentation, the longest axis of the egg is vertical, as Todd and Smart (1984) also observe. With $f(x) = 1$

Equation (1) gives a circle and with $f(x) = T < 1$ it gives an ellipse with its longest axis horizontal. In the latter case, T is the ratio of length of the minor and major axes of the ellipse. The next simplest function, with the two parameters T and a, is $f(x) = T(1 + ax)$, giving $y(x) = T(1+ax)\sqrt{1-x^2}$ which Preston called "Simple Ovoid"[2]. Here, T and a are to be estimated for the particular egg. Smart (1969, p153) and Todd and Smart (1984, Equation (3)) both asserted that this form provides a good representation of the shape for birds' eggs of many species but Preston (1953) did not share this opinion, preferring his three-parameter Equation (6a) which corresponds to $f(x) = T(1 + ax + bx^2)$, and which he called "Standard Avian Egg-Shape." Both Preston (1953) and Todd and Smart (1984) note that for pyriform eggs, f needs to be a cubic to give a good representation of the shape. When a cubic is needed, Preston called the (pyriform) shape "Alcid Ovoid." Preston (1953) and Todd and Smart (1984) recognized that higher order polynomials could be used in place of the cubic but comment that they found no need for this additional flexibility. Our experience is similar. Thus, the general egg shape, suitable for all bird species, is adequately represented by

$$y(x) = T(1+ax+bx^2+cx^3)\sqrt{1-x^2}. \tag{2}$$

It is important to appreciate that, when the parameters T, a, b, and c are chosen to suit the particular egg, the fit is so good that for all practical purposes, these four parameters perfectly capture the shape of the egg, as the results here illustrate.

Carter (1968) proposed a two-parameter formula which can be cast in the form of Equation (1); details can be seen in Supporting Information Section SupM1. The third parameter in that paper's title is simply the egg's length and so is unrelated to shape. Baker (2002, Equation (2)) also proposed a two-parameter formula for egg shape, given by

$$y(x) = T(1+x)^{1/(1+\lambda)}(1-x)^{\lambda/(1+\lambda)}, \tag{3}$$

and this formula is the one used by Stoddard et al. (2017). It can be cast into the general framework provided by Equation (1) as

$$y(x) = T\left(\frac{1+x}{1-x}\right)^{(1-\lambda)/(2(1+\lambda))}\sqrt{1-x^2}. \tag{4}$$

Troscianko (2014, Equation (1)) offered a three-parameter egg shape formula that becomes

$$y(x) = Te^{-\alpha x-\beta x^2}\sqrt{1-x^2} \tag{5}$$

when cast into the general framework. More details on the derivation of Equations (4) and (5) can be found in Supporting Information Section SupM1.

Baker's, Carter's, and Troscianko's formulae have two, two, and three parameters, respectively, compared to the four in Equation (2) that were found necessary to capture the full range of egg shapes in Preston (1953) and Todd and Smart (1984). The fit of Baker's formula to pyriform eggs in particular is markedly less satisfactory than Preston's proposal with a cubic.

As formulated here, in all of these models the parameter T is the ratio of the diameter of the egg at the midpoint of its length (referred to as "the equatorial diameter" by Preston (1968, p457)) to the length of the egg — as can be deduced by putting $x = 0$ in the formulae and using that the egg's length is two. Smaller values of T correspond to more elongated eggs.

In a somewhat different approach, Carter and Morley Jones (1970, Equation (5)) propose a formula based on polar coordinates with four parameters for shape and one for size, so it is comparable in complexity with Equation (2). They also give interpretations for their shape coefficients (calling them indices of aspect, skewness, marilynia, and platycephaly). Their suggestion does not seem to be expressible in the form of Equation (1), so details of the formulation are deferred to Supporting Information Section SupM3.

2.2 | Fitting Preston's parameters – underlying theory

The egg image is arranged so that its longest axis is horizontal, and it is assumed here that this is the $y = 0$ axis and that the egg has been scaled so that its poles are at $x = -1$ and $x = 1$. Then, the coordinates of the top and bottom edge of the egg are obtained. (More details on this and on the R program for fitting, which uses EBImage (Pau, Fuchs, Sklyar, Boutros, & Huber, 2010) for image processing, are in Supporting Information Section SupM5.) The y values for the bottom edge are reflected in the x-axis. Then, for each x value, x_i, this gives two y values: y_{i1} from the top and y_{i2} from the bottom.

Now, the obvious model for relating the data to Equation (1) is

$$y_{ij} = f(x_i)\sqrt{1-x_i^2} + \epsilon_{ij} \quad i = 1, \ldots, N,\ j = 1,2$$

where ϵ_{ij} are the errors and N is the number of points on each meridian. Then the error sum of squares is

$$\sum_{i=1}^{N}\sum_{j=1}^{2}\left(y_{ij} - f(x_i)\sqrt{1-x_i^2}\right)^2.$$

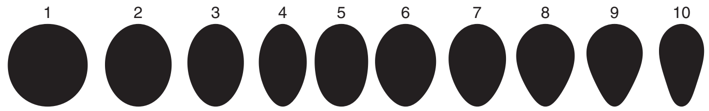
Minimizing the error sum of squares is the natural way to fit the parameters to a particular egg profile: this method is used here in all cases. When f is a polynomial, we have a linear model — more specifically, a multiple regression without a constant term — and so standard fitting can be used, which is what Preston (1953) did.

Rather than following Preston on fitting, Todd and Smart (1984) shift attention to

$$Y_{ij} = \frac{y_{ij}}{\sqrt{1-x_i^2}}$$

and therefore implicitly propose the model

$$Y_{ij} = \frac{y_{ij}}{\sqrt{1-x_i^2}} = c_0 + c_1x_i + c_2x_i^2 + c_3x_i^3 + \ldots + \frac{\epsilon_{ij}}{\sqrt{1-x_i^2}}.$$



	1	2	3	4	5	6	7	8	9	10
Elongation:	1.035	1.246	1.477	1.748	1.560	1.363	1.450	1.424	1.482	1.861
Pointedness:	0.501	0.508	0.534	0.539	0.545	0.547	0.579	0.616	0.650	0.675
PolarAsymmetry:	1.003	1.085	1.252	1.348	1.255	1.640	1.904	2.871	3.695	2.635

FIGURE 1 The values of the three shape indices for eggs of varied shapes. All egg images are scaled to have the same length. Key: (1) White-breasted Kingfisher (*Halcyon smyrnensis*); (2) Adélie penguin (*Pygoscelis adeliae*); (3) Dalmatian Pelican (*Pelecanus crispus*); (4) Greater Flamingo (*Phoenicopterus roseus*); (5) Southern Brown Kiwi (*Apteryx australis*); (6) Little Grebe (*Tachybaptus ruficollis*); (7) Royal Tern (*Thalasseus maximus*); (8) King Penguin (*Aptenodytes patagonicus*); (9) Pheasant-tailed Jacana (*Hydrophasianus chirurgus*); (10) Common Guillemot (*Uria aalge*)

This can be fitted as a linear model by weighted least squares — although the fitting process is not addressed in Todd and Smart (1984). The weights are proportional to the inverse of the variance of the errors and so will be $(1-x_i^2)$. This fitting process is equivalent to the linear model employed by Preston. Note too that c_0 is just T in the formulation in Equation (2). We will refer to (c_0, c_1, c_2, c_3) as Preston parameters.

To ensure the stability of the fitting process and allow high order polynomials to be used, the appropriate orthogonal polynomials are used, instead of fitting with simple powers of x_i. These are the Ultraspherical (Gegenbaur) polynomials for weight function $(1-x^2)$ (see Suetin, 2002). The details of this, which involves the introduction of another parametrization for the same egg formula which has some attractive features and which yields a simple formula for the egg volume, are described in Supporting Information Section SupM2. These alternative parameters will also be referred to as Preston parameters.

2.3 | Assessing fit

Once Preston parameters have been obtained, the egg shape they correspond to can be plotted and we call this the Preston fit. To assess the fit, the discrepancy between the Preston fit and the actual outline of the egg needs to be quantified. The measure of the quality of a fit proposed here is the square root of the average squared discrepancy between the actual egg and the fitted egg, after scaling the egg to have length one: essentially the root mean square error. This gives an error that is a length on the scale where the egg length is one. Thus, in the notation developed here, the error of a method is

$$\text{error}=\sqrt{\frac{1}{8N}\sum_{i=1}^{N}\sum_{j=1}^{2}\left(y_{ij}-e_{ij}\right)^2} \tag{6}$$

where e_{ij} is the fitted value corresponding to y_{ij} and obtained from the least squares fit of the parameters, and N is the number of points on the egg's meridian, or equivalently the number of x_i values. For photographs with good resolution, N is large and then this formula will be an accurate representation of the discrepancy between the fitted egg and the actual egg shape. In order to compare the quality of the fit of other models with Preston's (1953) model, we need to fit them by least squares too: we indicate how this was done in Supporting Information Section SupM3.

The methods are then compared, in Sections 3.1 and 3.2, using their errors defined by Equation (6).

In fitting Equation (4), Baker (2002) and Stoddard et al. (2017) propose excluding eggs where the fit is poor. Both seem close to suggesting the square of the error defined at Equation (6) to measure the quality of the fit, but neither explain exactly how to accommodate different values of N and they propose slightly different exclusion rules.

2.4 | Adding parameters to egg formulae

The beauty of Preston's proposal is that it provides an essentially exact representation for any egg shape using four parameters. It is

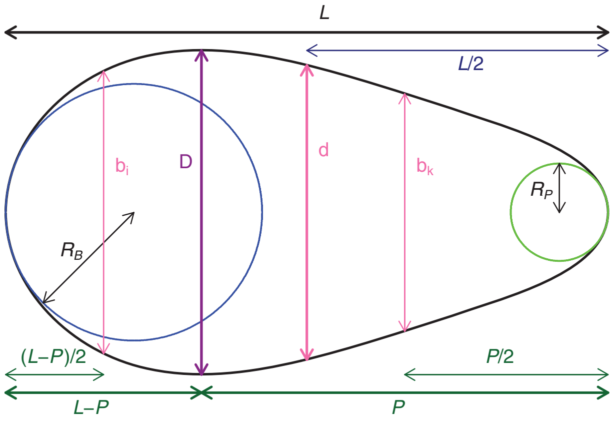


FIGURE 2 Graphical explanation of the symbols occurring in the text: L is the length of the egg; D is the largest latitudinal diameter; P is the length from the latitude of maximum diameter to the more distant pole; d is the equatorial diameter; R_B and R_P are the radii of the largest circles within the egg and touching the blunt and pointed pole, respectively; and b_i and b_k are the latitudinal diameter half way between the latitude of largest diameter and the blunt and pointed pole — b_i is the larger of the two

TABLE 1 Various shape indices; symbols defined in Figure 2; "Circle" gives the value of the index for a circle

Source	Index name	Formula	Circle
Length to breadth indices			
Preston (1968, p456)	elongation	D/L	1
Stoddard et al. (2017, SM-p4)	ellipticity	$(L/d) - 1$	0
Present study	Elongation	L/D	1
Departure of widest latitude from equator			
Belopol'skii (1957, p131)	Unnamed	$P/(L - P)$	1
Harris and Birkhead (1985, p174)	Shape index 1	$L/(L - P)$	2
Mänd et al. (1986, p614)	ovoidness	$P/(L - P)$	1
Deeming and Ruta (2014, p2)	asymmetry ratio	P/L	0.5
Present study	Pointedness	P/L	0.5
Model based asymmetry			
Stoddard et al. (2017, SM-p4)	asymmetry	$\lambda - 1$ (from eqn (4))	0
Comparisons of the egg poles			
Preston (1968, equation (6))	asymmetry	$\left(\sqrt{R_B} - \sqrt{R_P}\right)\sqrt{L/2}/d$	0
Preston (1968, equation (7))	bicone	$\left((\sqrt{R_B} + \sqrt{R_P})\sqrt{L/2}/d\right) - 1$	0
Preston (1968, equation (10))	Asymmetry	$(R_B - R_P)L/D^2$	0
Preston (1968, equation (11))	Bicone	$((R_B + R_P)L/D^2) - 1$	0
Mityay et al. (2015, p93)	asymmetry	R_P/R_B	1
Mytiai and Matsyura (2017, p265)	asymmetry	$(R_B - R_P)/D$	0
	infundibular	R_B/D	1
	cloacal	R_P/D	1
	interpolar	$(L - (R_B + R_P))/D$	0
	complementarity	$\dfrac{(1 + R_B/L)(1 + R_P/L)}{1 - R_B/L - R_P/L}$	∞
Present study	Polar Asymmetry	R_B/R_P	1
Comparisons using intermediate latitudes			
Mänd et al. (1986, p614)	pear-shapedness	$(b_i - b_k)/b_i$	0
	conidity	$(b_i - b_k)/D$	0
	blunt-end convexity	$(2b_i/D) - 1$	$\sqrt{3} - 1$
	sharp-end convexity	$(2b_k/D) - 1$	$\sqrt{3} - 1$
Using egg volume V			
Mänd et al. (1986, p614)	plumpness	$3V/(4\pi LD^2)$	1

natural to wonder whether the fits of the alternative models are improved markedly by adding parameters. It is straightforward to put additional parameters into the models of Carter (1968), Baker (2002) and Troscianko (2014). Thus, for Troscianko's formula the natural extension is

$$y(x) = Te^{-\alpha x - \beta x^2 - \gamma x^3}\sqrt{1 - x^2}. \qquad (7)$$

For Baker's model, one way to introduce the extra parameters is

$$y(x) = T(1 + x)^{1/(1+\lambda)}(1 - x)^{\lambda/(1+\lambda)}(1 + ax + bx^2), \qquad (8)$$

whilst for Carter's, an analogous possibility is given in Supporting Information Equation (SEq2). In each case, this increases the number of parameters to four, giving them similar flexibility to Equation (2), so that the errors for these extensions are expected to be roughly comparable with Preston's.

2.5 | Three shape indices

Preston's four-parameter representation of egg shape is so good that it can replace the silhouette, allowing images to be replaced by a simple accurate summary. However, these parameters are not easily interpretable as intuitive aspects of an egg's shape. A variety of indices has been proposed that are more easily interpretable and intended to reflect aspects of shape that are considered biologically important or interesting. We first introduce three egg shape indices we refer to as Elongation, Pointedness, and Polar Asymmetry.

Elongation is the ratio of the length to the width at the widest point. This is not the same as $1/T$, which uses the width at the midpoint of the egg's length (i.e. at the equator), rather than at the widest point.

Pointedness is the length from the point where the egg is widest to the more distant end divided by the overall length.

Polar Asymmetry is the ratio of the diameter of the largest circle that can fit within the egg outline and touch the egg at its blunt pole to the diameter of the largest circle within the egg outline and touching the more pointed pole.

Larger values of these indices correspond to greater departures from a circular shape. The values of these indices for eggs of particularly varied shapes are shown in Figure 1. For some nearly symmetrical eggs, the pole with the smaller circle (the more pointed end) can be the one that is nearer to the latitude where the egg is widest, which is the opposite of what might be expected: this is the case for egg 2 in Figure 1.

2.6 | Other shape indices

We now review other indices that have been proposed. Figure 2 is a graphical representation of the symbols used in this section and Table 1 is a summary of a selection of indices.

2.6.1 | Length to breadth indices

The first, and most obvious, index is what is called elongation (by, for example, example, Preston, 1968, p456): the ratio of the length of the largest latitudinal diameter (D) – often simply called its maximum diameter or breadth – to the length (L) of the egg. In this study, Elongation is defined as the reciprocal of elongation, so that its values are always ≥1, and larger values correspond to more elongation.

As an alternative to elongation, the ratio of the equatorial diameter (d) to the length of the egg could be used: d/L. This is the parameter T in the formulae in Section 2.1. It is ≤1 and is one for a circle. Thus, $1/T$ is ≥1, with larger values corresponding to less and less spherical eggs and $1/T$ agrees with Elongation for eggs which have their maximum diameter at their equator. Stoddard et al. (2017) use this index, with T obtained via Equation (4), but subtract one from it to make zero correspond to a circle. Thus, their index, which they call ellipticity, is $(1/T) - 1$, which in terms of direct egg measurements is $(L/d) - 1$ and in Preston parameters is $(1/c_0) - 1$.

2.6.2 | Departure of widest latitude from equator

In asymmetric eggs, the latitude of the maximum diameter will be displaced from the equator. That leads naturally to seeking a second index based on this displacement. In this study, we use Pointedness: the length from the latitude of maximum diameter to the more distant pole (P) divided by the overall length (L). Similar indices have been used by Belopol'skii (1957), Harris and Birkhead (1985) and Mänd et al. (1986). Their proposals are all monotonic transformations of Pointedness and so are equivalent to it (in that they will have a perfect Spearman correlation with Pointedness). The same index, called the asymmetry ratio, has been proposed by Deeming and Ruta (2014, p2)[3] where "equatorial axis" is the latitude of maximum diameter (which is not the sense of "equatorial" here) — so their definition is indeed identical to that of Pointedness.

2.6.3 | Model based asymmetry

Stoddard et al. (2017) define their asymmetry index to be $\lambda - 1$ having fitted the formula (4) to the egg profile. The −1 is to make the value of the index zero for a circle. (In fact, they use $\max\{\lambda, 1/\lambda\} - 1$ to deal properly with nearly symmetrical cases, but this is a minor refinement.) The main difficulty with this index is that the model in Equation (4) (i.e. Baker, 2002) does not fit well in all cases (see Section 3).

2.6.4 | Comparisons of the egg's poles

A variety of proposals exist for indices based on the curvature of the poles of the egg. Preston (1968, p456) notes that even for symmetrical eggs, the two ends can be more or less pointed: "both ends may be conspicuously pointed as in the tinamous, or they may both be conspicuously blunt as in the hummingbirds." Thus, he sought an index that could reflect this difference, which he called bicone. In addition, and less subtly, there can be asymmetry, with the curvature of the two poles being markedly different. Based on this thinking and his modeling Preston (1968, Equation (6), Equation (7)) proposed two indices, bicone and asymmetry, derived from the curvature at the poles. He made various approximations and simplifications to derive alternative indices (Preston, 1968, Equation (10), Equation (11)), which he calls Bicone and Asymmetry, that were easier to obtain through field measurements, although as mentioned above, these entailed the use of a spherometer. Now that photographs can be more easily analyzed, finding the largest circle within the egg and touching its pole provides a sensible alternative to using a spherometer.

In order to describe the indices based on the curvature at the poles, we follow Preston's (1968) terminology: let R_B and R_P be the radii of the largest circle at the blunt and the pointed end, respectively, as illustrated in Figure 2. It is now straightforward to obtain versions of Preston's indices, either in their original form or in his operational substitutions. Although their approach is rather different, Mityay et al. (2015), Mityay, Strigunov, and Matsyura (2016) and Mytiai and Matsyura (2017) also suggest a variety of indices based on the radii of circles. They are not fully consistent in naming these nor in the formulae. In particular, the "index of asymmetry" in Mityay et al. (2015) is R_P/R_B, the reciprocal of Polar Asymmetry, but the "index of asymmetry" in Mytiai and Matsyura (2017) is different: it is $(R_B - R_P)/D$. A selection of indices from Mytiai and Matsyura (2017) is included in Table 1.

2.6.5 | Comparisons using intermediate latitudes

Instead of using the curvature of the poles, Mänd et al. (1986) define indices[4] based on the diameters for the latitudes midway between the latitude of largest diameter and the two poles. Let b_i and b_k be these two latitudinal diameters, with b_i being the larger of the two. In Mänd et al. (1986, Figure 3) and in Figure 2, the larger diameter, b_i, is obtained from the latitude nearer to the blunt pole, and this is typical. However, in nearly symmetrical eggs the larger diameter can be nearer the more pointed pole, a possibility which Mänd et al. (1986) may not have envisaged. The definition used in this study makes b_i the larger of the two intermediate diameters even in these cases.

Mänd et al.'s (1986) pear-shapedness and conidity are based on the difference in these two distances, so will both be zero for any symmetrical egg. For an asymmetrical egg, b_k will be less than b_i, with larger values of these indices corresponding to greater asymmetry. The other two indices, blunt-end convexity and sharp-end convexity, seek to measure the pointedness of each end separately and so are similar in spirit to Mytiai and Matsyura's (2017) infundibular and cloacal.

2.6.6 | Using egg volume

Mänd et al. (1986) propose an index which compares the egg volume, V, to that of a prolate ellipsoid (i.e. one with circular cross-sections on the minor axis). They proposed $400V/(\pi LD^2)$. In Table 1, the multiplier has been adjusted to give an index value of one if the egg shape was an ellipse with major axis L and minor axis D.

2.6.7 | Scaling and centering of indices

A shape index is, necessarily, independent of size and so has no length scale. By considering the value that the index will take for a circle, the index can be rescaled so that a circle gives a value of one or re-centered to make the value for a circle zero. For example, Stoddard et al. (2017) subtracted one from $1/T$ and from λ to make the value for a circle zero and Preston (1968) subtracts one in the definition of Bicone for the same reason. Such maneuvers make no essential difference but do lead to some of the differences in naming and definitions. Here, the scaling of Mänd et al.'s (1986) pear-shapedness and conidity has been adjusted: the originals were 100 times the formulae in Table 1.

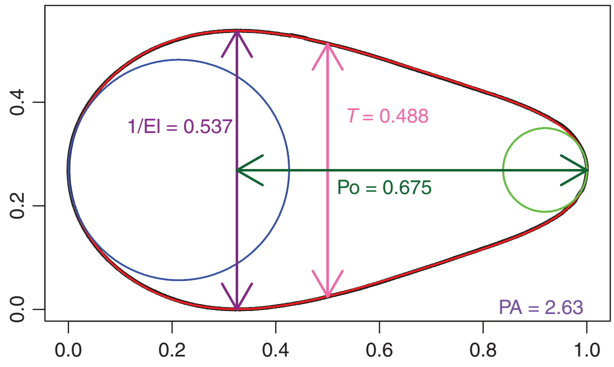


FIGURE 3 The actual egg shape of C126 is the black outline; the Preston fit is in red. The error, as defined at Equation (6), is 0.00091. The length of the egg has been scaled to be one. The two circles are the largest possible that touch the end of the egg and are wholly within the (Preston fit to the) egg. Then, the Polar Asymmetry (PA) is the ratio of the diameter of the larger (blue) to the smaller (green) circle. Po is the pointedness. EI is the Elongation. T is the equatorial diameter

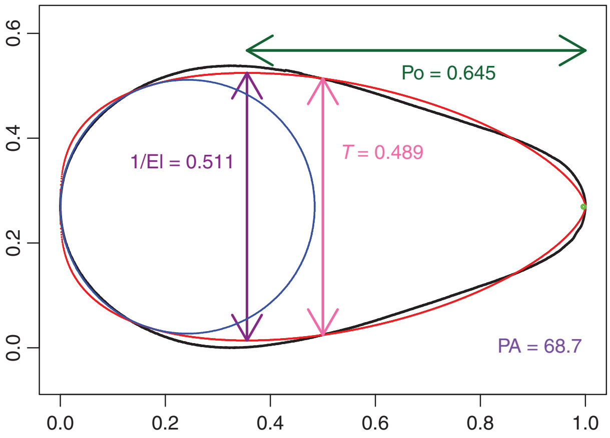


FIGURE 4 The actual egg shape of C126 is the black outline; the Baker fit is in red. The error, as defined at Equation (6), is 0.0116. The values of Po, 1/EI, and T based on the Baker fit are indicated. The Polar Asymmetry (PA) is very large because of the very small circle at the more pointed end

2.6.8 | Data driven index-like summaries

Once egg profiles are in a standard orientation (which here is horizontal, with the x-axis along the longest axis) and size (which here is the maximum length standardized to be two), a collection of coordinates on the profile taken at a fixed collection of x-values is a multivariate observation on an egg profile. As such, techniques like principal components can be used to explore and summarize shape. This is, in essence, the approach used in Deeming and Ruta (2014) and Deeming (2017). In particular, Deeming and Ruta (2014) perform a principal component analysis on a wide range of egg shapes and observe that the first principal component is highly correlated with elongation and the second with their asymmetry ratio and that the first two components account for 89.48% and 7.96%, respectively, of the total variance, confirming that these two indices account for much of the variation in egg shape; Deeming (2017) explores the relationship of various factors on these principal components over a large selection of bird species.

2.7 | Egg characteristics from Preston parameters

Figure 2 is a graphical representation of the measurements that are used to define various indices. All of these can be obtained from the

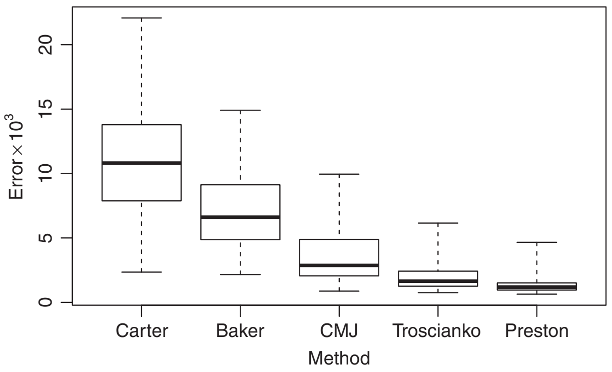


FIGURE 5 Boxplots comparing the error defined at Equation (6) (multiplied by 1,000) for the methods of Carter (1968), given in Supporting Information Equation (SEq1), the methods of Baker (2002) and Troscianko (2014), given in Equations (4) and (5), the method of Carter and Morley Jones (1970), described in Supporting Information Equation (SEq6), labeled CMJ, and the method of Preston (1953) given in Equation (2). The results are for 132 eggs of various species: 18 *Uria aalge*, 16 *Uria lomvia*, 7 *Alca torda*, 11 *Aptenodytes patagonicus*, 10 *Lanius collurio*, 10 *Phalacrocorax carbo*, 10 *Gallus gallus domesticus*, 10 *Spheniscus humboldti*, 10 *Eudyptes pachyrhynchus*, 30 *Larus fuscus*. The heavy line is the median, the boxes extend between the upper and lower quartiles, the whiskers extend to the minimum and maximum

Preston parameters: the two radii, R_B and R_P, are the most complicated to obtain, but are easily found by a suitable search procedure. Furthermore, assuming circular cross-sections, the formula for egg shape can also be used to find other egg characteristics: for example, the surface area, volume, or "contact index" (as in Birkhead, Thompson, Jackson, et al., 2017), which indicates how much of an egg resting naturally makes contact with the substrate. In particular, Supporting Information Equation (SEq4) shows how to obtain the egg volume from the Preston parameters. It is also straightforward to fit the alternative models, for example that in Equation (4), to the Preston fit for the egg, instead of going back to the original photograph. As the Preston fit is so good, this produces parameters very similar to those obtained from fitting to the photograph directly, as is illustrated in Supporting Information Section SupM4. Thus, the various indices in Table 1 can be readily obtained from the Preston parameters. In a similar vein, the approach in Deeming and Ruta (2014) can be applied to the shapes obtained from the Preston parameters of a collection of eggs, rather than to the original photographs.

3 | RESULTS

3.1 | Comparisons using a pyriform egg

The focus here is on the avian egg shape that historically has been the most challenging: pyriform. A guillemot egg (labeled C126, see Supporting Information Figure SF10) was selected, because of its marked pyriform shape, to use as a test case for the various formulae. In Figure 3, the Preston fit is superimposed on the egg outline: both are plotted "thinly," so that the close fit is clear. The egg outline is drawn using the (x_i, y_{ij}) pairs introduced at the start of Section 2.2: there are $N = 3{,}488$ points on each meridian, so the egg outline based on them is, for practical purposes, exact. The error, as defined at Equation (6), is 0.00091. Various derived quantities (Elongation, Pointedness, Polar Asymmetry, and equatorial diameter) are also marked on the figure.

In Figure 4, the Baker fit is illustrated for the same egg. The fit is poor (the error, as defined at Equation (6), is 0.0116) and, if the Baker fit were used to estimate our derived quantities, several of them would be in error. As can be seen from Figure 4, Polar Asymmetry would be vastly overestimated, because of the excessively pointed end in the Baker fit. Elongation would be overestimated and Pointedness would be underestimated. For this egg, it looks as though the equatorial diameter would be accurately estimated through the Baker fit. Baker (2002) proposed omitting eggs like this, where the fit is poor, and that recommendation is followed by Stoddard et al. (2017, SM-p4, Figures S2 and S8.A). This is a serious drawback when applying the method to draw conclusions about the full range of avian egg shapes.

Comparing the fit in Figures 3 and 4, the error (given by Equation (6)) for the Baker fit (i.e. fitting Equation (4)) is more than 12 times that of the Preston fit. For comparison, the error for the Troscianko fit (i.e. fitting Equation (5) – illustrated graphically in Supporting Information Figure SF11) is five times that of the Preston error, and the error for the Carter fit (i.e. fitting Supporting Information Equation (SEq1)) is 17 times that of the Preston error. For egg C126, the four-parameter extensions in Equations (7) and (8) and Supporting Information Equation (SEq2) give errors that are, respectively, 1.8, 2.7, and 3.4 times the Preston error. These last three all correspond to good fits "by eye," as is illustrated in Supporting Information Figure SF12 for the one with the largest error (i.e. Supporting Information Equation (SEq1)) but they are still slightly poorer than the Preston fit. The method proposed by Carter and Morley Jones (1970) produces 10.7 times the Preston error and the fitted egg has visible undulations, illustrated in Supporting Information Figure SF13, and so does not accurately capture this egg's shape.

3.2 | Comparisons of fit over a selection of eggs

Figure 5 gives the errors of each method over a selection of 132 eggs from ten species. It shows that the errors from Preston's method are generally smaller than those of the others. The actual Preston errors range from 0.00064 to 0.00466, based on values of N that range from 1706 to 3622. Additional comparisons are included in Supporting Information Section SupM6. These show that when the proposals of Carter (1968), Baker (2002) and Troscianko (2014) are augmented to each have four parameters, as in Equations Supporting Information (SEq2), (8) and (7), respectively, they provide fits of comparable quality to Preston's.

For a circular egg profile, all methods work well, so Figures 5 and Supporting Information Figure SF2 cannot, and are not intended to, show that the difference in quality of the fit is important in all cases. Rather, they demonstrate that Preston's method is satisfactory for all eggs, including those where the alternatives proposed elsewhere work less well. Preston's method is the best choice for providing a consistently accurate summary over a range of egg shapes.

3.3 | The importance of egg position

The validity of the Preston summary relies on the egg being horizontal (i.e. the line through the poles being horizontal) when photographed. Otherwise, for example, the assumption of circular cross-section will be invalid and so using the Preston summary to obtain an egg volume will give an incorrect answer. Most birds' eggs do not rest naturally in a horizontal position. A pointed egg that is at rest will have its pointed end lower and its blunt end higher than would be the case if it were horizontal. Thus, the length will be foreshortened and so will be shortened when compared to the breadth. To explore the kind of biases this will introduce, data on 185 eggs of various species that were photographed in both the horizontal and in their resting position are compared in Supporting Information Section SupM7. It is clear from those results that marked biases are introduced if eggs in a resting position are used.

3.4 | Comparison of indices

For the three indices introduced here in Section 2.5, Elongation, Pointedness, and Polar Asymmetry, an interactive 3d-plot (Supplementary-Material2.html, see Data Accessibility) of their values on a large collection of eggs illustrates that, for pyriform eggs, each contains information not in the other two, as the cloud has marked scatter, regardless of the angle it is viewed from.

Preliminary observations on the relationships between various indices in Table 1 are in Supporting Information Section SupM8. The strength and form of these relationships will depend on the the collection of eggs used. As the main focus is dealing satisfactory with pyriform eggs, the main data used to compare the indices are on 735 *Uria aalge* eggs.

The shape of the correlation matrix in Supporting Information Figure SF7 shows four groups of indices, indicated by the high correlations near the diagonal. We identify indices that typify these groups. The first corresponds to Elongation, the second to Preston's (1968) bicone, the third to Pointedness, and the fourth to Polar Asymmetry. Thus, for the complexities of pyriform shape, just as four parameters are needed for the Preston fit, four shape indices capture different aspects of their shape. Of these four, Preston's (1968) bicone is rather different from the other three, in that it is an index of the average curvature at the two poles, and seems less directly related to the main features of the shape. The other three provide a satisfactory basis for comparisons of pointedness in a general sense.

4 | DISCUSSION

The demonstrated merits of Preston's approach to summarizing egg shape make it a proper starting point for all future studies that aim to capture egg shape closely. Using it as the basis of quantifying egg shape would allow the sorts of comparative study pioneered by Stoddard et al. (2017) to be conducted with rather more confidence.

The accuracy of the shape obtained means that the Preston parameters can be used to compute any desired biologically sensible indices without recourse to the original egg or its photograph. As noted already, other methods can provide an adequate summary of some eggs, but four parameters (as in Preston's method) are needed to be assured of a good summary of all eggs. Even if the fit of a method is not as good as Preston's, it may well be satisfactory for deriving with reasonable accuracy some egg characteristics. There will, for example, be only relatively minor differences in the estimate of egg volume based on different methods. However, in contrast, Polar Asymmetry is an example of an index where the parametric shape needs to mimic the shape of the actual egg closely at each pole to obtain an accurate estimate (c.f. Figures 3 and 4 and Supporting Information Figure SF11).

Given the effectiveness of Preston's approach, a database summarizing, through Preston parameters, a large collection of appropriately taken photographs of eggs would be a valuable resource for future research.

Errors of asymmetry and surface imperfections are incorporated into the error in the fitting. Thus, the consistently small errors found here for the four-parameter models (see Supporting Information Figure SF1: maximum 0.005, three-quarters below 0.002, where the egg has length one) indicate that these aspects are genuinely minor. There is a case for regarding a good smooth fit (like Preston's) to the egg shape as being its "real" shape, with biological significance, with minor imperfections being genuinely insignificant randomness.

The quality of the Preston fit means that the way the photographs are taken and the processing of the images are important. The method of taking photographs and the adjustment for lens distortion are described in Birkhead, Thompson, and Biggins (2017, Supplementary Material).

The three indices Elongation, Pointedness, and Polar Asymmetry each measure aspects of egg shape in an intuitive way. For pyriform eggs, the results show that each of these indices contributes information about the egg's shape that the other two do not. Of the other indices that have been proposed, none is clearly more suitable based on their correlations and the immediacy of interpretation. An extensive comparative study of the range of indices proposed across a full range of egg shapes would be needed to establish fully their relative merits, their commonalities, and their effectiveness at capturing biologically interesting aspects of shape.

5 | CONCLUSION

We demonstrate that the method proposed by Preston (1953), and revisited in Preston (1968) and Todd and Smart (1984), works accurately for all egg shapes and is better than the existing alternatives. The programs supplied provide a straightforward way to obtain the Preston parameters for a collection of suitable photographs and illustrate how to use these parameters to derive other egg characteristics. To use these methods, it is important that the photographs are of eggs positioned horizontally, otherwise biases are introduced. The present study establishes the value of using all three of the indices Elongation, Pointedness, and Polar Asymmetry when pyriform eggs are being considered.

ACKNOWLEDGMENTS

We thank all the museum curators, and Douglas Russell (Natural History Museum, Tring, UK) in particular, for their help and for allowing us to measure and photograph eggs in their collections. Thanks also to R. Montgomerie, J. Troscianko and an anonymous referee for useful comments on the MS. The work was funded in part by a grant from the Leverhulme Trust to TRB.

CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTIONS

TRB conceived the study; JDB and TRB wrote the paper; JET and TRB measured and photographed the eggs; and JDB did the mathematics and the programming.

DATA ACCESSIBILITY

The R programs described in Supporting Information Section SupM5 and suitable test data, an R script that generates all the analyses in this paper and the data sets used in the analyses, and the file Supplementary-Material2.html are available through Dryad, \https://doi.org/10.5061/dryad.8kv2b20.

ENDNOTES

[1] Sections in the document Supplementary Material, provided as Supporting Information, have the prefix SupM, figures have the prefix SF and equation numbers have the prefix SEq.

[2] It is worth nothing that Equation (4.1) in Okabe (1952) is "Simple Ovoid": Consequently, his approach to the bio-mechanical understanding of egg formation is automatically constrained to produce egg shapes in this class.

[3] A slightly different definition occurs in Deeming and Ruta (2014, figure 5, p9), but that one is incorrect (C. Deeming, pers com, January 2018).

[4] Mänd et al. (1986) mention that some of their indices were derived from those of Kostin (1977).

ORCID

John D. Biggins http://orcid.org/0000-0001-9310-261X

REFERENCES

Attard, M. R. G., Medina, I., Langmore, N. E., & Sherratt, E. (2017). Egg shape mimicry in parasitic cuckoos. *Journal of Evolutionary Biology*, *30*, 2079–2084. https://doi.org/10.1111/jeb.13176

Baker, D. E. (2002). A geometric method for determining shape of bird eggs. *The Auk*, *119*(4), 1179–1186. https://doi.org/10.1642/0004-8038(2002)119[1179:AGMFDS]2.0.CO;2

Bán, M., Barta, Z., Muñoz, A. R., Takasu, F., Nakamura, H., & Moskát, C. (2011). The analysis of common cuckoo's egg shape in relation to its hosts' in two geographically distant areas. *Journal of Zoology*, *284*, 77–83. https://doi.org/10.1111/j.1469-7998.2011.00795.x

Barta, Z., & Székely, T. (1997). The optimal shape of avian eggs. *Functional Ecology*, *11*, 656–662. https://doi.org/10.1046/j.1365-2435.1997.00136.x

Belopol'skii, L. O. (1957). *Ecology of sea colony birds of the Barents Sea*, Israel Program for Scientific Translations, Jerusalem (Translated from Russian 1961).

Birkhead, T. R., Thompson, J. E., & Biggins, J. D. (2017). Egg shape in the common guillemot *Uria aalge* and Brunnich's guillemot *U. lomvia*: Not a rolling matter. *Journal of Ornithology*, *158*, 679–685. https://doi.org/10.1007/s10336-017-1437-8

Birkhead, T. R., Thompson, J. E., Jackson, D., & Biggins, J. D. (2017). The point of a guillemot's egg. *IBIS*, *159*, 255–265. https://doi.org/10.1111/ibi.12458

Carter, T. C. (1968). The hen's egg: A mathematical model with three parameters. *British Poultry Science*, *9*, 165–171. https://doi.org/10.1080/00071666808415706

Carter, T. C., & Morley Jones, R. (1970). The hen's egg: Shell shape and size parameters and their interrelations. *British Poultry Science*, *11*, 179–188. https://doi.org/10.1080/00071667008415805

Deeming, D. C. (2017). Effect of composition on shape of bird eggs. *Journal of Avian Biology*, *49*, https://doi.org/10.1111/jav.01528

Deeming, D. C., & Ruta, M. (2014). Egg shape changes at the theropod-bird transition, and a morphometric study of amniote eggs. *Royal Society Open Science*, *1*(3), 140311. https://doi.org/10.1098/rsos.140311

Frantsevich, L. (2015). *'Planimetry of the egg shape parameters*. Retrieved from http://www.biometrica.tomsk.ru/planirus.htm, in Russian, English abstract.

Harris, M. P., & Birkhead, T. R. (1985). Breeding ecology of the Atlantic alcidae. In D. Nettleship, & T. R. Birkhead (Eds.), *The Atlantic Alcidae* (pp. 155–205). London, UK: Academic.

Köller, J. (2017). *Egg curves and ovals. Mathematische Basteleien*. Retrieved from http://www.mathematische-basteleien.de/eggcurves.htm

Kostin, J. V. (1977). On the methods of oomorphological studies and the unifying of the descriptions of oological materials. In G. A. Noskov (Ed.), *Metodiki issledovanija produktivnosty i struktury vidov ptits v predelah ih arealo* (pp. 14–22). Vilnius, Lithuania: Mokslas.

Mallock, A. (1925). The shapes of birds' eggs. *Nature*, *116*, 312–313.

Mänd, R., Nigul, A., & Sein, E. (1986). Oomorphology: A new method. *The Auk*, *103*, 613–617. https://www.jstor.org/stable/4087137

Mityay, I., Matsyura, A., & Jankowski, K. (2015). Application of bird egg morphometrics in phylogeny. *Acta Biologica Sibirica*, *1*(3–4), 92–102. https://doi.org/10.14258/abs.v1i3-4.914

Mityay, I., Strigunov, V. I., & Matsyura, A. V. (2016). Egg shape in the taxonomy and phylogeny of birds of prey. *Biological Bulletin of Bogdan Chmelnitskiy Melitopol State Pedagogical University*, *6*(3), 447–454.

Mónus, F., & Barta, Z. (2005). Repeatability analysis of egg shape in a wild tree sparrow (*Passer montanus*) population: A sensitive method for egg shape description. *Acta Zoologica Academiae Scientiarum Hungaricae*, *51*(2), 151–162.

Mytiai, I. S., & Matsyura, A. V. (2017). Geometrical standards in shapes of avian eggs. *Ukrainian Journal of Ecology*, *7*(3), 264–282. https://doi.org/10.15421/2017_78

Okabe, J. (1952). On the forms of hen's eggs. *Reports of the Research Institute for Applied Mechanics*, *1*, 17–32.

Pau, G., Fuchs, F., Sklyar, O., Boutros, M., & Huber, W. (2010). Ebimage—an R package for image processing with applications to cellular phenotypes. *Bioinformatics*, *26*(7), 979–981. https://doi.org/10.1093/bioinformatics/btq046

Preston, F. W. (1953). The shapes of birds' eggs. *The Auk*, *70*, 160–182. https://doi.org/10.2307/4081145

Preston, F. W. (1968). The shapes of birds' eggs: Mathematical aspects. *The Auk*, *85*, 454–463. https://doi.org/10.2307/4083294

Preston, F. W. (1969). Shapes of birds' eggs: Extant North American families. *The Auk*, *86*, 246–264. https://doi.org/10.2307/4083498

Romanoff, A. L., & Romanoff, A. J. (1949). *The avian egg*. New York, NY: Wiley.

Smart, I. H. M. (1969). The method of transformed co-ordinates applied to the deformations produced by the walls of a tubular viscus on a contained body: The avian egg as a model system. *Journal of Anatomy*, *104*(3), 507–518.

Stoddard, M. C., Yong, E. H., Akkaynak, D., Sheard, C., Tobias, J. A., & Mahadevan, L. (2017). Avian egg shape: Form, function, and evolution. *Science*, *365*(6344), 1249–1254. https://doi.org/10.1126/science.aaj1945

Suetin, P. K. (2002). *Ultraspherical polynomials*, Originally published in Encyclopaedia of Mathematics, Springer. Retrieved from https://www.encyclopediaofmath.org/index.php/Ultraspherical_polynomials.

Thompson, D. W. (1942). *On growth and form*. Cambridge, UK: Cambridge University Press.

Todd, P. H., & Smart, I. H. M. (1984). The shape of birds' eggs. *Journal of Theoretical Biology*, *106*, 239–243. https://doi.org/10.1016/0022-5193(84)90021-3

Troscianko, J. (2014). A simple tool for calculating egg shape, volume and surface area from digital images. *IBIS*, *156*, 874–878. https://doi.org/10.1111/ibi.12177

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Biggins JD, Thompson JE, Birkhead TR. Accurately quantifying the shape of birds' eggs. *Ecol Evol*. 2018;8:9728–9738. https://doi.org/10.1002/ece3.4412

CHAPTER 3:

Wade’s Birds of Bempton Cliffs and his observations on Guillemot (*Uria aalge*) eggs

Wade's Birds of Bempton Cliffs and his observations on Guillemot (*Uria aalge*) eggs

Birkhead, T. R. and Thompson, J. E. (2019). *Archives of Natural History*, **46**, 240-252.

Original article can be found using the link below:

https://www.euppublishing.com/doi/10.3366/anh.2019.0588

Chapter context and thesis author's contributions: This chapter presents a published article in Archives of Natural History that provides an historical account of the life and work of Edward Walter Wade, a regular collector of Common Guillemot eggs at Bempton Cliffs on the North Yorkshire coast during the early 20th Century. Wade was a climber and this paper highlights how his direct observations and interactions with breeding Common Guillemots led him to question the validity of a previous popular explanation for the Common guillemot's pyriform egg: the 'spin-like-a-spinning-top' hypothesis. Here, we place Wade's observations into the wider context of previous research examining the adaptive function(s) of the pyriform shape of Common Guillemot eggs and emphasise the importance of direct observations and experiences of natural breeding environments when developing biologically meaningful and relevant adaptive explanations for egg shape.

For this published article, I conducted the research into E.W. Wade's family history, previous occupations and life events. This required me to examine and investigate various ancestry records and obituary articles, amongst other resources. Additionally, I located and collated E.W. Wade's complete bibliography. I also provided comments and assistance with subsequent re-drafts of the manuscript.

Co-author's contributions: T.R. Birkhead conceived the idea for the manuscript. T.R. Birkhead wrote the initial draft of the manuscript and contributed to the research for this published article.

Archives of Natural History 46.2 (2019): 240–252
Edinburgh University Press
DOI: 10.3366/anh.2019.0588

www.euppublishing.com/anh

Wade's *Birds of Bempton Cliffs* and his observations on Guillemot (*Uria aalge*) eggs

T. R. BIRKHEAD and J. E. THOMPSON

Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
(e-mail: T.R.Birkhead@sheffield.ac.uk)

ABSTRACT: Edward Walter Wade (1864–1937), author of *The Birds of Bempton Cliffs* (1903, 1907), is almost unknown. He worked as a clerk for the family timber company in Hull and in his spare time visited Bempton Cliffs, where he climbed (routinely without a rope) to observe the seabirds and to collect eggs. He was an active member of the Hull Scientific and Field Naturalists' Club and became one of their Vice-Presidents and President. Between 1902 and 1920 he was a member of the British Ornithologists' Union. Wade's published comments on guillemots and their pyriform-shaped eggs, at Bempton, were unusually insightful, in part because his observations were made at close range (a consequence of his climbing ability), and partly because he thought carefully about what he saw. Wade was among the first to point out that the spinning-like-a-top explanation for the guillemot's pyriform egg shape was incorrect based on his own observations. An appendix lists Wade's 69 articles, mostly about birds in Yorkshire, published between 1901 and 1930.

KEYWORDS: Flamborough – oology – pyriform eggs – Hull Scientific and Field Naturalists' Club – bibliography.

INTRODUCTION

The seabird colony at Bempton Cliffs on the Flamborough Headland, Yorkshire, has a long history of exploitation. For centuries the Common Guillemot (*Uria aalge*, hereafter Guillemot), Razorbill (*Alca torda*), Atlantic Puffin (*Fratercula arctica*) and Kittiwake (*Rissa tridactyla*), breeding on the vertical chalk cliffs (up to 120 metres high), were exploited for their eggs (Vaughan 1998). As was common throughout the Northern Hemisphere (Fisher and Lockley 1954), eggs (and undoubtedly some adult birds) were taken at Bempton for human consumption. From the early 1800s, as the scientific hobby of egg collecting (known as oology) became increasingly popular, collectors (and dealers) converged on Bempton Cliffs to purchase seabird eggs from the 'climmers' (climbers) who harvested tens of thousands of eggs each year (Vaughan 1998). Guillemot eggs were particularly popular with collectors because of their large size, seemingly infinite variety of colour and markings, and their unusual pointed shape (Whitaker 1997; Birkhead 2016; Birkhead and Montgomerie 2018). Known as 'climming', the process of obtaining seabird eggs on the Flamborough peninsula became a popular tourist attraction, and much has been written about it both in the popular press and the ornithological literature (Waterton 1835; Yarrell 1871; Seebohm 1883, 1885; Nelson 1907; Vaughan 1998; Ellis 2014).

Although the climmers sometimes allowed tourists to descend parts of the cliff to collect eggs for themselves, there was little crossover between the climming and collecting cultures. As a result, there was a curious disconnect between the climmers and the collectors. The former

Figure 1. Edward Walter Wade, date unknown (from Varty 1991: 30; reproduced by permission of the Yorkshire Naturalists' Union, York).

were uneducated labourers from the farms adjacent to the cliffs, who supplemented their modest income by collecting eggs at the weekends and evenings and selling them, especially to collectors. The climmers had no interest in the eggs themselves, except perhaps as items to eat. As one said: "we didn't want eggs, we wanted money" (cited in Kightly 1984: 90). The collectors, on the other hand were better educated and relatively wealthy. The climmers had first-hand experience with the birds and their eggs on the cliffs; the collectors relied on the climmers for information about the location of particularly desirable eggs, and about the 'biology' of the birds. For example, the ornithologist and oologist Henry Seebohm recounted details (such as the belief that Guillemots lay the same coloured egg each year) told to him by a veteran climmer, George Londesborough, nicknamed 'Old Lowney' (Seebohm 1885).

A notable exception to this was Edward Walter Wade (1864–1937) (Figure 1). Virtually unknown today, Wade was described as a "climber of skill and daring" and "a scientific recorder, and the historian of the bird lore of this famed headland [Flamborough]" (Ravenscliffe 1938: 33)[1]. Known as 'Sandy' (Ravenscliffe 1938), Wade was born in June 1864 at Eastoft, near Scunthorpe, Lincolnshire. His father, George Frederick Wade, graduated from St John's, Cambridge, with a BA in 1848 and served as vicar of St Lawrence, York, between 1867 and 1882. G. F. Wade married Mary Hinchliffe in 1855; they produced a brood of seven offspring: two girls and five boys. In 1880, at the age of 15 or 16, Sandy Wade left school to join the family firm of Richard Wade and Sons, timber importers and creosoters (artisans treating timber with the preservative creosote) in Hull, for whom he worked until his retirement in March 1929. After his father died in 1882, Sandy Wade continued to live at home with his mother, sisters, an aunt and two servants at 325 Anlaby Road, Hull. At the age of 44, Sandy Wade married Helen Phillips Brodrick in April 1909; they had one daughter, Mary Brodrick Wade. The 1911 Census noted that the Wade family employed two young (aged 16 and 23) women as servants, suggesting that they

Figure 2. Yorkshire Naturalists' Union during their excursion to Filey in 1903 (*The Naturalist* 1903: plate VIIA). Edward Walter Wade is indicated by the white arrow. (Reproduced by permission of the Yorkshire Naturalists' Union, York.)

were reasonably well off. The 1901 Census listed "E. W. Wade" as a timber merchant, and the 1911 Census as a merchant's clerk. He retired to Dorset, and died, aged 73, on 12 July 1937 (Anonymous 1937a, 1937b).

From the 1890s, Sandy Wade was clearly interested in birds, and became a member of the Hull Scientific and Field Naturalists' Club. In the Society's report for 1903–1906 he is listed as one of their Vice-Presidents (Anonymous 1907), and Sheppard (1910: 8) stated that around 1910 he was President of that Society. Wade was also involved with the Yorkshire Naturalists' Union (YNU), being a member of their Protection Committee from 1906 until 1927 (Varty 1991), as well as attending a number of their organized excursions (Figure 2). Wade became a member of the British Ornithologists' Union (BOU) in 1902 (Anonymous 1902: xx); the last mention of him as a member of the BOU is 1920 (where his address was listed as Melton Road, North Ferriby, E. Yorks. [Anonymous 1920: xxv]). Wade was described as having a "fine weather-hardened face", a "genial good nature" and an "East Yorkshire accent" (Ravenscliffe 1938). He was clearly a regular visitor to Bempton Cliffs, where he shocked the climmers by scaling the cliffs without the protection of a safety rope – something the climmers would never have contemplated.

Writing of his climbing at Bempton, Wade (1903, 1907) himself wrote:

> I have aroused no little astonishment and some wrath by my supposed foolhardiness. I have been likened to a rat (with an adjective) running about the rocks, and one Sunday morning, after an arduous climb up some very loose rock, on arriving at the top who should I meet but my old friend Ned Hodgson [a climmer], with his grandson in one hand and his "bonny blackthorn" [stick] in the other. Shaking the latter at me, he exclaimed, "Eh, A 'd a good manhd tee warm yer".

Wade's head for heights meant that he also assisted other oologists, notably the surgeon Edward S. Steward (1871–1954), whom he accompanied to Scotland in February 1908 to obtain the eggs of Crossbills, *Loxia scotia*, and Golden Eagles, *Aquila chrysaetos* (Cole and Trobe 2000: 240) and again in April 1912 for Golden Eagles. "Wade lost no time in … climbing … to the nest, which was on top of a flat rock, sheer below and at the sides. Wade's task was easy. He climbed above the nest, then let himself down on to it by means of a rowan, where he stood and signalled – two eggs" (Steward 1988).

It was Wade's climbing ability that gave him an unusual insight into the Guillemot's world on the cliffs at Bempton, allowing him to comment with some authority on several aspects of this species' biology. He gave several talks on birds to the Hull Scientific and Field Naturalists' Club, including one on birds and their nests, another on "Ornithological rambles in Holland", and one entitled "The Birds of Bempton Cliffs" in 1902. Wade also published a number of very short articles on birds and other topics between 1900 and 1918 in *British Birds* and in *The Naturalist* between 1911 and 1930, including two accounts of the deaths of two climmers – men he undoubtedly knew (Wade 1923) – one from natural causes and one killed on the cliffs (Wade 1910, 1911). In September 1922 the British Association for the Advancement of Science met in Hull, and Wade, either persuaded or invited by Thomas Sheppard (1876–1945), the curator of Hull Museum, produced a comprehensive summary of the birds of East Yorkshire (Wade 1922). Between 1910 and 1930, he published, in *The Naturalist*, an annual summary of the birds seen in the East Riding that, among much else, included comments on the incidence of oiled seabirds, changes in the Kittiwake population at Bempton, and events associated with the Bempton climming. In his annual report for 1924, Wade (1925) stated that:

> The persistent taking of all well-marked [Guillemot and possibly Razorbill] eggs at Bempton has resulted in the practical elimination of such specimens. It is impossible even to guess how long it has taken to evolve these types, which have been known for at least fifty years, but the intensive hunt for them during about thirty years has at last done its work.

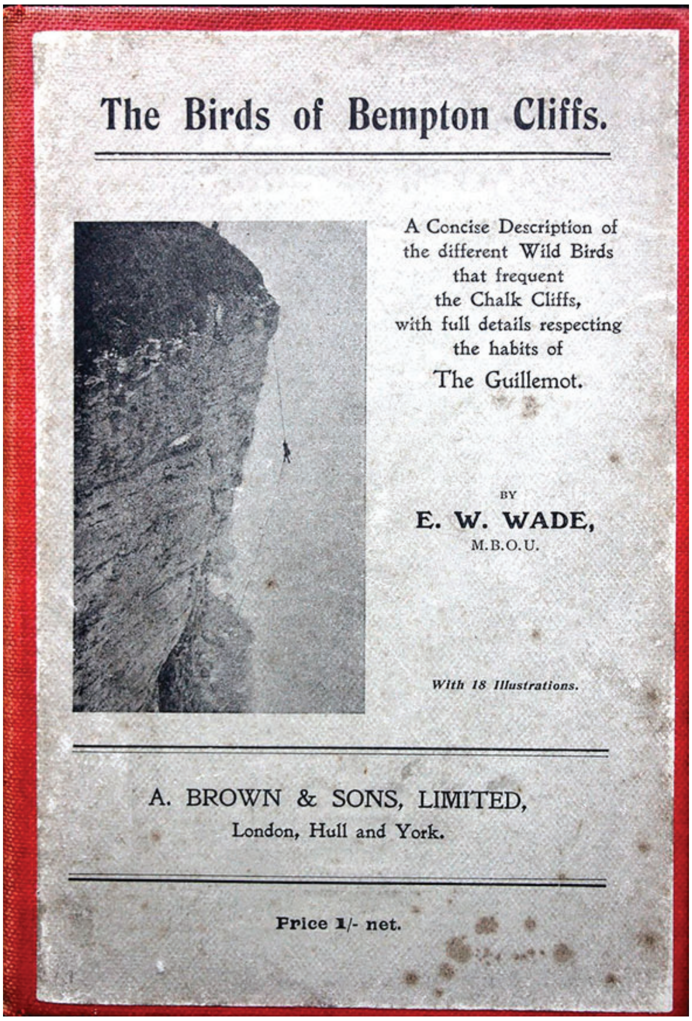
Wade was correct that the removal of unusual eggs such as rare red eggs (Birkhead and Montgomerie 2018), year after year, and in some cases probably over particular females' entire lifespans, undoubtedly reduced the likelihood of those birds (assuming egg colour is inherited) passing on their egg traits to their daughters (Wade 1925).

Edward Walter Wade died on 12 July 1937. His death was reported in two "In Memoriam" that same year in *The Naturalist* (Anonymous 1937c; Foster *et al.* 1937), and a further two the subsequent year in *Bird Notes and News* (Ravenscliffe 1938) and the Yorkshire Naturalists' Union Report for 1937, reported in *The Naturalist* (Anonymous 1938). As Foster *et al.* (1937) touchingly noted about the death of Wade: "Wild Nature has lost a fine historian."

THE BIRDS OF BEMPTON CLIFFS

As a result of his remarkable climbing skills, Wade had the unusual opportunity to observe the Guillemots and other seabirds at close range on their breeding ledges. He also made his own collection of eggs, including Guillemot eggs from Bempton, which appear to have been presented to the Hull Museum (Sheppard 1910). However, the collection and other archival material relating to Wade was destroyed during the bombing of Hull in the Second World War.[2]

Wade's talk on Bempton to the Hull Scientific and Field Naturalists' Club in 1902 resulted in the written account in the society's *Transactions* (Wade 1903); it was subsequently reproduced as a separate publication, under the same title, in 1907 (Figure 3). Both versions are



The Birds of Bempton Cliffs.

A Concise Description of
the different Wild Birds
that frequent
the Chalk Cliffs,
with full details respecting
the habits of
The Guillemot.

BY
E. W. WADE,
M.B.O.U.

With 18 Illustrations.

A. BROWN & SONS, LIMITED,
London, Hull and York.

Price 1/- net.

Figure 3. *Birds of Bempton Cliffs* 1907.

identical; both are illustrated with photographs of the cliffs, climmers and seabirds. Where we cite page numbers, we do so from the 1907 version.

Briefly, the article and booklet cover the following topics:

1. The various seabird protection acts of 1880, 1881, 1894 and 1896 (the shooting of Kittiwakes and the blowing of hooters by ships to scare the birds from the cliffs – to entertain the tourists – had been a problem). Eggs however, were not protected.
2. The grandeur of the Flamborough Cliffs, and the fact that the climmers had named every headland or point (the location of some of these points are given in Vaughan [1998]). Interestingly, the editor of the *Transactions of the Hull Scientific and Field Naturalists' Club* had added a footnote to this section of the text (Wade 1903) that one point of the cliffs had recently become known as "Wade's Spot". Its location, however is not currently known.
3. Guillemot laying dates – this information presumably came at least partly from the climmers' accumulated knowledge.
4. The time taken for Guillemots to produce a replacement egg: 19–20 days. This figure however, is incorrect. Most estimates, including those from other egg collectors (for example, Rickaby, cited in Whitaker 1997) and subsequent biologists, are around 14 days (Gaston and Jones 1998).

5. Wade stated that the Guillemot's egg is laid blunt end first. This is incorrect. Our personal observations of some 30 laying females shows that in every case the egg is laid pointed end first. It is worth noting that almost all of Wade's observations of Guillemot behaviour were made on birds disturbed (that is, flushed off their eggs) every three or four days throughout the season by the climmers (and by Wade himself), so it is hardly surprising that he (and the climmers) sometimes made mistakes or misinterpreted the birds' biology. For example, Wade commented that "many" Guillemot eggs were laid at sea and were trawled up in Filey Bay (six to eight kilometres from Bempton). This is clearly non-adaptive, and we interpret this as a consequence of the regular disturbance by the climmers, keeping some females away from their site at the time they would normally have laid.

Wade reported on eggs of similar colour and markings, presumed to be laid by the same female, taken from the same spot over twelve to 14 years. Wade himself had egg specimens from the same site for nine consecutive years. The climmers knew that female Guillemots used the same site (roughly ten centimetres across, as one of us [TRB] has personally observed) year after year, sometimes for 20 consecutive years, and hence were long-lived, and produced a similar egg (in terms of colour and pattern) each time. He estimated the numbers of eggs collected annually (including first and one or two successive layings of replacement eggs) by the climmers to be about 130,000 – the same figure is given in Nelson (1907), who may have been parrotting Wade (1903). Subsequent researchers have suggested that this figure was too high, but it was still in the tens of thousands (Vaughan 1998; Birkhead 2016). Wade described the culture and the process of climming, stating that it "is doubtless familiar to many readers, but I have so often seen it inaccurately described that I should like to go over the ground again". Some of this information and some of Wade's photographs are also reproduced in Nelson's (1907) *Birds of Yorkshire*.

Wade (1907) was intrigued by the fact that Guillemots persist in coming back to the same site year on year "however much persecuted". He also commented on the remarkable variation in the colour and markings of Guillemot eggs, stating: "The colouring of these birds' eggs also opens up many different problems." He was referring here to the biological aspects of egg colouration and cites Charles Dixon's introductory text to the second volume (1884) of *A History of British Birds* by Henry Seebohm (1832–1895):

> A word as to the marvellous variation and beautiful colours of the eggs of the guillemot. The extraordinary amount of variation in the colour of these eggs appears to be a grave difficulty, and one which utterly refuses to conform to those laws that govern the tints with which so many birds' eggs are adorned. It is one of those very few instances where Nature has seemingly run riot in her variations. … Why, we are apt to ask, do the guillemots's eggs vary so considerably?

Dixon then explained that the absence of predators means that "they [Guillemots] have few enemies of their eggs … and the variations that occur are of small moment." Dixon's argument here is based on the writings of Alfred Russel Wallace (1832–1913) on the evolution of egg colour in birds. Wallace (1889) suggested that because Guillemots have no predators (because they breed on inaccessible cliff ledges) there was no need for their eggs to be cryptically or uniformly similar in colour. The idea is nonsense, because, as Wade pointed out, even though Guillemots breed in accessible places, gulls are serious predators of their eggs (Birkhead 2016). It is now known that the extraordinary variation in Guillemot egg colour and patterning is an adaptation to breeding at very high densities and facilitates the recognition of eggs by their parents (Tschanz 1990). It is with regard to the Guillemot's unusually shaped egg however, that Wade is most perceptive.

WADE ON EGGS

Wade (1907) wrote:

> The peculiar pear-shape of the Guillemot's egg, in conjunction with its position upon the rock ledges, lends itself to the belief that it has been evolved by the law of the survival of the fittest, as it would obviously be a protection against the destruction of the egg by the agency of the wind.

He was referring here to an idea proposed first (as far as we can tell) by the oologist William Hewitson (1806–1878): that the Guillemot's pyriform egg provides protection from falling, by spinning like a top. Hewitson (1831) had written:

> Were the eggs of the guillemot shaped like those of the majority of birds, nothing could save them; their form, which is peculiar to themselves amongst the eggs of the seafowl, is their only protection; it gives them greater steadiness when at rest, and where they have room to roll, the larger end moving round the smaller in a circle, keeps them in their original position.

This idea was repeated and slightly extended by Francis Orpen Morris (1810–1893) in his extremely popular *History of British Birds* (1856): "The shape of the egg, which is very tapering, prevents it from rolling off into the sea; for when moved by the wind, or other circumstances, it only rolls round in its own circle, without changing its first immediate situation." Hewitson's idea was that the pyriform shape of the Guillemot's egg allows it to rotate on the spot; Morris's addition is "when moved by the wind", and it is this idea of what Wade (1907: 21) referred to as "destruction of the egg by the agency of the wind" that he commented on: "Upon this point, however, there is room for controversy, as an examination of the actual conditions now prevailing leaves a doubt whether this abnormal [that is, pyriform] shape could have been so developed."

Wade (1907: 21) stated that "constant observation and enquiry have failed to elicit any instance of an egg revolving on its own axis" and that the surface of the Guillemots' breeding ledges are so uneven "as almost to prevent such movement". He also added (correctly) that under normal circumstances Guillemots almost never leave their egg unattended, implying that their eggs are unlikely to be exposed to the wind, and moreover even during a gale, the ledges where the birds breed are calm, "shielded from the fury of the wind, apparently by an air buffer covering the face of the rock, from which the force of the gale rebounds". Finally, Wade (1907: 22) stated that on the Farne Islands, where:

> eggs are laid on the top of an unsheltered stack of rock, there is no recorded observation of their eggs being blown about by the wind, nor has this open position produced any special modification in the shape of the egg, which exactly resembles those laid in sheltered places.

Wade thus dismissed the idea that the pyriform shape of the Guillemot's egg has evolved to allow it to rotate on its axis when blown by the wind. As pointed out elsewhere (Birkhead 2016, 2017), Hewitson (1831) almost certainly based his spinning-like-a-top idea on the behaviour of an empty (and hence very light) eggshell. As is easily demonstrated, an empty Guillemot eggshell can be made to spin on its axis, and is so light it is easy to imagine it being moved by the wind. A natural egg full of yolk and albumen or an embryo is heavier and cannot be moved in this way. Wade does not offer any alternative suggestions for why Guillemot eggs are pyriform in shape.

Wade's perceptive comments about egg shape came about because of his direct experience of observing Guillemot eggs on the breeding ledges, whereas almost all others that wrote about Guillemot egg shape were collectors whose experience was limited to intact eggs handed to them by the climmers, and to the blown eggs in their collections. The only other person to have previously made such discerning remarks on this topic was the Scottish ornithologist William MacGillivray (1796–1852), who in his *A History of British Birds* (1852) stated that: "A very little inequality suffices to steady an egg [of a Guillemot], and it is further prevented from rolling over by its pyriform shape, which however has not all the effects generally supposed." MacGillivray does not elaborate, but it seems that, like Wade, he was far from convinced by Hewitson's 'spinning-like-a-top' idea. Seebohm (1885: **3**: 397) wrote something similar: "The supposition that the egg of the guillemot is so formed as to turn round on its own axis, instead of rolling over the rocks, is a mere fanciful theory", but, again, he does not elaborate. It seems plausible that MacGillivray's and Seebohm's comments (which may not be independent) may have inspired Wade to think about the problem.

Later, Russian biologists studying Guillemot egg shape during the 1920s through to the 1940s also rejected Hewitson's idea (Birkhead 2016). Kaftanovskii was credited (Belopol'skii 1961: 132) as stating in 1941: "It is not true that murre [that is, Guillemot] eggs resemble tops which merely spin around on the spot at every push or wind movement (as sometimes noted in the popular literature)." Despite the fact that the spinning-like-a-top idea was based on empty eggshells and therefore biologically irrelevant, this erroneous idea continues to persist in the popular literature, on the internet and in the public imagination (Birkhead 2016: ix).

The adaptive significance of the Guillemot's egg shape was later thought to have been identified by Russian biologists, who concluded that the pyriform shape allowed the egg to roll in an arc (rather that rotating on the spot), thereby minimizing the risk of rolling off the cliff edge (Birkhead 2016).[3] Even though a Guillemot's pyriform egg will indeed roll in an arc on a smooth and gently sloping surface, very extensive testing by Paul Ingold (1980) provided no convincing evidence that a Guillemot egg was any less likely to roll off a ledge than the more elliptical and rounded egg of a Razorbill (Birkhead *et al.* 2017a, 2017b). The rolling-in-an-arc idea, nevertheless, remains widespread. Two recent, alternative suggestions for the pyriform shape include: (1) because of the way a pyriform egg lies on the substrate, the blunt end of the egg remains relatively free from contamination by the dirt and faeces that characterise Guillemot breeding ledges, allowing the embryo to respire; (2) a pyriform egg may, together with a thick shell, provide the strength to allow Guillemots to incubate on bare rock ledges with no nest, and where frequent interactions with neighbours means that eggs may be vulnerable to physical damage (Birkhead *et al.* 2017b). These two hypotheses are difficult to test, and while it is clear that a pyriform shape keeps the blunt end of a Guillemot egg relatively clean, it is difficult to establish whether avoiding dirt is the main selective force favouring this shape. There is convincing evidence, however, for a third hypothesis: that the Guillemot's pyriform egg is inherently stable, especially on a sloping ledge, allowing the egg to be more safely manipulated by the parents during incubation and incubation change-overs (Birkhead *et al.* 2018a, 2018b; Birkhead 2019). This stability, a result of the greater proportion of the egg's surface being in contact with the substrate, means that it is less likely to roll in the first place (Birkhead 2019).

CONCLUSION

Edward Walter Wade was an active, informed and productive amateur ornithologist whose 'local patch' comprised the East Riding of Yorkshire, and in particular the huge seabird colony at Bempton Cliffs on the Flamborough Headland. Wade was very unusual among those interested in the activities of the 'climmers' and the biology of the Guillemot breeding at

Bempton Cliffs in that, unlike most other egg collectors, he also climbed the cliffs to gain access to seabird eggs. Wade thought carefully about his observations and appears to have been among the first to explicitly state that the spinning-like-a-top idea as an explanation for the Guillemot's unusual, pyriform egg shape, was incorrect.

ACKNOWLEDGEMENTS

We thank Keith Clarkson, Linda Ellis, Paula Gentil, Debbie Hall (*The Hull Daily Mail*), Roger Riddington, Douglas Russell (Natural History Museum, Tring), Jeff Wardlow and Jim Whitaker for helping us locate images and valuable discussions. Special thanks to the Yorkshire Naturalists' Union Committee for their assistance and for granting us permission to use photographs of Sandy Wade in this paper. We also thank Ms R. Mallalieu for advice and Douglas Russell for useful comments on the manuscript.

NOTES

[1] Ravenscliffe was the nom-de-plume of William Henry Hamer (1869–1940) (see index to *Bird Notes and News* **18**. 1938), a Bridlington-based engineer and a member of the Royal Society for the Protection of Birds. He later moved to New Zealand, where he continued to write about birds (Anonymous 1940). He clearly knew of Sandy Wade, but it is not known whether they were friends.

[2] Paula Gentil to Douglas Russell, pers. comm., 3 July 2017; Paula Gentil to TRB, pers. comm., 14 July 2017.

[3] Wade (1907) alluded to this idea too, without identifying it explicitly, when he said that the parent Guillemot usually leaves its egg with the pointed end orientated towards the sea and often at the extreme edge of the ledge, such that if it were to roll it "must inevitably fall".

REFERENCES

ANONYMOUS, 1902. British Ornithologists' Union. 1902. *Ibis* (eighth series) **2**: vi–xxiii.

ANONYMOUS, 1907. List of officers, 1906–07. *Transactions of the Hull Scientific and Field Naturalists' Club* **3**: unpaginated.

ANONYMOUS, 1920. List of the members of the British Ornithologists' Union. 1920. *Ibis* (eleventh series) **2**: v–xxix.

ANONYMOUS, 1937a. Death of Mr E. W. Wade: former Hull authority on bird life. *The Hull Daily Mail*, 14 July, p. 5.

ANONYMOUS, 1937b. Deaths: Wade. *The Yorkshire Post*, 14 July, p. [1].

ANONYMOUS, 1937c. In memoriam: Edward Walter Wade. *The Naturalist* **1937**: 194.

ANONYMOUS, 1938. Yorkshire Naturalists' Union: annual report, 1937. Obituary. *The Naturalist* **1938**: 35.

ANONYMOUS, 1940. Obituary: William Henry Hamer. *Journal of the Institution of Civil Engineers* **15**: 71.

BELOPOL'SKII, L. O., 1961. *Ecology of Sea Colony Birds of the Barents Sea*. R. Ettinger and C. Salzmann, translators. Jerusalem.

BIRKHEAD, T. R., 2016. *The Most Perfect Thing: the Inside and Outside of a Bird's Egg*. London.

BIRKHEAD, T. R., 2017. Vulgar errors: the point of a guillemot's egg, or why the widely believed explanation for the guillemot's pointed egg is almost certainly wrong. *British Birds* **110**: 456–467.

BIRKHEAD, T. R., 2019. The shapes of birds' eggs. *British Birds* **112**: 122–124.

BIRKHEAD, T. R., and R. MONTGOMERIE, 2018. Rare red eggs of the Common Guillemot (*Uria aalge*): birds, biology and people at Bempton, Yorkshire, in the early 1900s. *Archives of Natural History* **45**: 69–79.

BIRKHEAD, T. R., J. E. THOMPSON and J. D. BIGGINS, 2017a. Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: not a rolling matter? *Journal of Ornithology* **158**: 679–685.

BIRKHEAD, T. R., J. E. THOMPSON, D. JACKSON and J. D. BIGGINS, 2017b. The point of a Guillemot's egg. *Ibis* **159**: 255–265.

BIRKHEAD, T. R., J. E. THOMPSON and R. MONTGOMERIE, 2018a. The pyriform egg of the common murre *Uria aalge* is more stable on sloping surfaces. *Auk Ornithological Advances* **135**: 1020–1032.

BIRKHEAD, T. R., J. E. THOMPSON, J. D. BIGGINS and R. MONTGOMERIE, 2018b. The evolution of egg shape in birds: selection during the incubation period. *Ibis*. https://doi.org/10.1111/ibi.12658 (accessed 8 March 2019).

COLE, A. C., and W. M. TROBE, 2000. *The Egg Collectors of Great Britain and Ireland*. Leeds.

ELLIS, Linda, 2014. *Bempton Cliff Climbing*. Bridlington.

FISHER, James, and R. M. LOCKLEY, 1954. *Sea-birds*. London

FOSTER, H. M., C. W. MASON, C. F. PROCTOR and T. STAINFORTH, 1937. The late E. W. Wade. *The Naturalist* **1937**: 268.

GASTON, A. J., and I. JONES, 1998. *The Auks*. Oxford

HEWITSON, William C., 1831. *British Oology: Being Illustrations of the Eggs of British Birds*. Newcastle upon Tyne.

INGOLD, Paul, 1980. Anpassungen der Eier und des Brutverhaltens von Trottellummen *Uria aalge aalge* Pont. an das Brüten auf Felssimsen. *Zeitschrift für Tierpsychologie* **53**: 341–388.

KIGHTLY, Charles, 1984. *Country Voices: Life and Lore in Farm and Village*. London.

MacGILLIVRAY, William, 1852. *A History of British Birds*. London.

MORRIS, F. O., 1856. *A History of British Birds*. London.

NELSON, Thomas H., 1907. *The Birds of Yorkshire*. London.

RAVENSCLIFFE [HAMER, W. H.], 1938. The Birds of Bempton Cliffs. *Bird Notes and News* **18**: 33–37, 64–66.

SEEBOHM, Henry, 1883. *A History of British Birds, with Coloured Illustrations of their Eggs*. Volume 1. London.

SEEBOHM, Henry, 1884. *A History of British Birds, with Coloured Illustrations of their Eggs*. Volume 2. London

SEEBOHM, Henry, 1885. *A History of British Birds, with Coloured Illustrations of their Eggs*. Volume 3. London

SHEPPARD, Thomas, 1910. *Guide to the Birds in the Hull Municipal Museum*. Hull Museum Publications No. 75. Hull.

STEWARD, Edward Simmons, 1988. *The journal of Edward Simmons Steward FRCS, MBOU*. Leeds.

TSCHANZ, Beat, 1990. Adaptations for breeding in Atlantic alcids. *Netherlands Journal of Zoology* **40**: 688–710.

VARTY, Clive G., 1991. *Yorkshire Naturalists' Union Protection of Birds Committee Centenary Year 1891–1991*. Otley.

VAUGHAN, Richard, 1998. *Seabird City: a Guide to the Breeding Seabirds of the Flamborough Headland*. Otley.

WADE, E. W., 1903. The birds of Bempton Cliffs. *Transactions of the Hull Scientific and Field Naturalists' Club* **3**: 1–26.

WADE, E. W., 1907. *The Birds of Bempton Cliffs: a Concise Description of the Different Species of Wild Birds that Frequent the Chalk Cliffs, with Full Details Respecting the Habits of the Guillemot*. Second edition. London, Hull and York.

WADE, E. W., 1910. A veteran 'climmer'. *The Naturalist* **1910**: 373–375.

WADE, E. W., 1911. The accident on the Bempton Cliffs. The *Naturalist* **1911**: 102–103.

WADE, E. W., 1922. Birds of East Yorkshire.T. Sheppard, editor. *Handbook to Hull and the East Riding of Yorkshire*. Pp 333–351. London and Hull.

WADE, E. W., 1923. The Fulmar in Yorkshire. *The Naturalist* **1923**: 350.

WADE, E. W., 1925. Yorkshire Naturalists' Union: annual report, 1924. Vertebrate Zoology, East Riding. *The Naturalist* **1925**: 25–26.

WALLACE, Alfred Russel, 1889. *Darwinism: an Exposition of the Theory of Natural Selection, with Some of its Applications.* London and New York.

WATERTON, Charles, 1835. Notes on a visit to the haunts of the guillemot and facts on its habits. *Magazine of Natural History* **8**: 162–165

WHITAKER, James, 1997. *A Diary of Bempton Climbers*. Leeds.

YARRELL, William, 1871. *A History of British Birds.* Fourth edition. Volume 1. London.

Received 21 December 2017. Accepted 31 May 2018.

APPENDIX: Bibliography for E. W. Wade.

To the best of our knowledge, below is the complete bibliography of Edward Walter Wade. The bibliography was collated through the use of Google Scholar and Web of Knowledge data base searches, as well as manually searching *British Birds*, *The Naturalist*, and *Transactions of the Hull Scientific and Field Naturalists' Club* that E. W. Wade was a regular contributor to. We searched publications from these journals for the years 1890 through 1937 inclusive, when Wade was a member of the Hull Scientific and Field Naturalists' Club (until his death in 1937).

1. 1901. The Black Rat (*Mus rattus*) at Hull. *Transactions of the Hull Scientific and Field Naturalists' Club* **1**: 232.
2. 1903. The Birds of Bempton Cliffs. *Transactions of the Hull Scientific and Field Naturalists' Club* **3**: 1–26.
3. 1907. *The Birds of Bempton Cliffs: a Concise Description of the Different Species of Wild Birds that Frequent the Chalk Cliffs, with Full Details Respecting the Habits of the Guillemot.* Second edition. London, Hull and York.
4. 1907. The Peregrines at Bempton. *The Naturalist* **1907**: 216.
5. 1907. Quail in East Yorks. *The Naturalist* **1907**: 255.
6. 1907. Yorkshire naturalists at the South Cave. Vertebrate Zoology. *The Naturalist* **1907**: 286–287.
7. 1907. East Yorkshire bird notes, 1907. *The Naturalist* **1907**: 419–422.
8. 1908. A Yorkshire Peregrine. *The Naturalist* **1908**: 360.
9. 1908. The breeding habits of the Common Bittern. *British Birds* **1**: 329–334.
10. 1909. On the status of the Stone Curlew in Yorkshire. *The Naturalist* **1909**: 11–16.
11. 1909. A veteran 'climmer'. *The Naturalist* **1909**: 373–375.
12. 1909. The Peregrine Falcon on the Yorkshire cliffs. *British Birds* **3**: 85.
13. 1910. Glossy Ibis in Holderness. *The Naturalist* **1910**: 28.
14. 1910. Unseasonable nesting dates. *The Naturalist* **1910**: 28.
15. 1910. Yorkshire Naturalists' Union: annual report, 1909. Vertebrate Zoology Section, East Riding. *The Naturalist* **1910**: 40–45.
16. 1910. Peregrines at Bempton. *The Naturalist* **1910**: 245.
17. 1910. East Yorkshire migration notes. *The Naturalist* **1910**: 277.
18. 1910. The natural history of Spurn. Ornithology. *The Naturalist* **1910**: 342.
19. 1911. Yorkshire Naturalists' Union: annual report, 1910. Vertebrate Zoology Section, East Riding. *The Naturalist* **1911**: 41–44.
20. 1911. The accident on the Bempton Cliffs. *The Naturalist* **1911**: 102–103.
21. 1911. Another occurrence of the Glossy Ibis in Yorkshire. *The Naturalist* **1911**: 116.
22. 1912. Yorkshire Naturalists' Union: annual report, 1911. Sections and committees. Vertebrate Zoology Section, East Riding. *The Naturalist* **1912**: 20–21.
23. 1912. Black-bellied Dipper at Bridlington. *The Naturalist* **1912**: 57.

24. 1913. Yorkshire Naturalists' Union: annual report, 1912. Vertebrate Zoology Section, The East Riding. *The Naturalist* **1913**: 75–76.
25. 1913. Glossy Ibis in Holderness. *The Naturalist* **1913**: 115.
26. 1913. Little Auks in Holderness. *The Naturalist* **1913**: 115.
27. 1913. Peregrines at Bempton. *The Naturalist* **1913**: 260.
28. 1913. Diminution of Starlings in Yorkshire. *British Birds* **7**: 178.
29. 1914. Unusual winter migration of Woodcock. *British Birds* **7**: 324–327.
30. 1914. Great Shearwaters at St. Kilda. *British Birds* **8**: 76.
31. 1914. Status of the Land-rail in Yorkshire. *British Birds* **8**: 150.
32. 1914. Yorkshire Naturalists' Union: annual report, 1913. Vertebrate Zoology Section, East Riding. *The Naturalist* **1914**: 25–26.
33. 1914. Waxwings in East Yorkshire. *The Naturalist* **1914**: 99.
34. 1914. Nesting habits of the Stone Curlew. *The Naturalist* **1914**: 123–124.
35. 1915. Yorkshire Naturalists' Union: annual report, 1914. Vertebrate Zoology Section, East Riding. *The Naturalist* **1915**: 36–37.
36. 1915. [with A. HAIGH-LUMBY] Yorkshire Naturalists at Hambleton. Vertebrate Zoology. *The Naturalist* **1915**: 265.
37. 1916. Yorkshire Naturalists' Union: annual report, 1915. Vertebrate Zoology Section, East Riding. *The Naturalist* **1916**: 33–34.
38. 1917. Yorkshire Naturalists' Union: annual report, 1916. Vertebrate Zoology Section, East Riding. *The Naturalist* **1917**: 37–38.
39. 1918. Yorkshire Naturalists' Union: annual report, 1917. Vertebrate Zoology Section, East Riding. *The Naturalist* **1918**: 36–37.
40. 1918. The Bempton Peregrines. *The Naturalist* **1918**: 257.
41. 1919. Yorkshire Naturalists' Union: annual report, 1918. Vertebrate Zoology Section, East Riding. *The Naturalist* **1919**: 35–36.
42. 1919. Yorkshire Naturalists at Spurn. Birds. *The Naturalist* **1919**: 387– 388.
43. 1920. Yorkshire Naturalists' Union: annual report, 1919. Vertebrate Zoology Section, East Riding. *The Naturalist* **1920**: 39–40.
44. 1920. Crossbills in East Yorks. *The Naturalist* **1920**: 106.
45. 1920. Note on Little Owl. *The Naturalist* **1920**: 140–141.
46. 1920. Yorkshire Naturalists at Beverley. Birds. *The Naturalist* **1920**: 390.
47. 1921. Yorkshire Naturalists' Union: annual report, 1920. Vertebrate Zoology Section, East Riding. *The Naturalist* **1921**: 35–36.
48. 1921. Migratory movements of birds near Hull. *The Naturalist* **1921**: 101–103.
49. 1921. Rose-coloured Starlings in Holderness. *The Naturalist* **1921**: 134.
50. 1921. Territory in bird life. *The Naturalist* **1921**: 418.
51. 1922. Birds of East Yorkshire. T. Sheppard, editor. *Handbook to Hull and the East Riding of Yorkshire*. Pp 333–351. London and Hull.
52. 1922. Yorkshire Naturalists' Union: annual report, 1921. Vertebrate Zoology Section, East Riding. *The Naturalist* **1922**: 36–37.
53. 1922. Extending range of the Fulmar Petrel. *The Naturalist* **1922**: 223–224.
54. 1922. Hoopoe in East Yorks. *The Naturalist* **1922**: 299.
55. 1923. Yorkshire Naturalists' Union: annual report, 1922. Vertebrate Zoology Section, East Riding. *The Naturalist* **1923**: 30–31.
56. 1923. The Fulmar in Yorkshire. *The Naturalist* **1923**: 350.
57. 1924. Yorkshire Naturalists' Union: annual report, 1923. Vertebrate Zoology Section, East Riding. *The Naturalist* **1924**: 26.
58. 1925. Yorkshire Naturalists' Union: annual report, 1924. Vertebrate Zoology Section, East Riding. *The Naturalist* **1925**: 25–26.
59. 1926. Yorkshire Naturalists' Union: annual report, 1925. Vertebrate Zoology Section, East Riding. *The Naturalist* **1926**: 9–10.
60. 1927. An inland migration of Grey Geese. *British Birds* **21**: 162–163.
61. 1927. Yorkshire Naturalists' Union: annual report, 1926. Vertebrate Zoology Committee, East Riding. *The Naturalist* **1927**: 18–19.
62. 1928. Yorkshire Naturalists' Union: annual report, 1927. Vertebrate Zoology Committee, East Riding. *The Naturalist* **1928**: 59–60, 81.
63. 1928. Yorkshire Naturalists at Spurn. Vertebrate Zoology. *The Naturalist* **1928**: 315.

64. 1928. Clouded Yellow Butterfly in Holderness. *The Naturalist* **1928**: 342.
65. 1929. A plea for the Heron. *The Naturalist* **1929**: 47–49.
66. 1929. Yorkshire Naturalists' Union: annual report, 1928. Vertebrate Zoology Committee, East Riding. *The Naturalist* **1929**: 79–81.
67. 1929. Dark Green Fritillary × Meadow. *The Naturalist* **1929**: 334.
68. 1930. Yorkshire Naturalists' Union: annual report, 1929. Zoological Section, East Riding. *The Naturalist* **1930**: 76–78.
69. 1930. Yorkshire Naturalists' Union. The 356th meeting (Vertebrate Zoology Section). *The Naturalist* **1930** (supplement): xv.

CHAPTER 4:

Egg shape in the Common Guillemot *Uria aalge* and Brünnich’s Guillemot *U. lomvia*: not a rolling matter?

Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: not a rolling matter?

Birkhead, T. R., Thompson, J. E. and Biggins, J. D. (2017). *Journal of Ornithology*, **158**, 679-685.

Original article and Supplementary Materials can be found using the link below:

https://link.springer.com/article/10.1007/s10336-017-1437-8

Chapter context and thesis author's contributions: One of the most comprehensive study of the rolling-in-an-arc hypothesis of the adaptive significance of the pyriform egg shape in the two *Uria* species (Brünnich's Guillemot and Common Guillemot) was conducted by Ingold (1980), but provided limited evidence for that hypothesis. In that study, Ingold addressed an apparent anomaly in that Brünnich's Guillemot eggs are less pyriform than those of the Common Guillemot, despite breeding on narrower ledges. He suggested that Brünnich's Guillemots could 'get away with' producing less pyriform eggs because their eggs are smaller than those of Common Guillemots and that, since he had found an interaction between mass and rolling arc characteristics, this explained the apparent anomaly. This study set out – using eggs sourced from museum collections and fieldwork – to test the idea that Brünnich's Guillemots eggs are smaller than those of Common Guillemots, and found that they are not. The lack of evidence to support this previous explanation by Ingold (1980) in turn further raises questions about the plausibility of the popular rolling-in-an-arc adaptive explanation for the pyriform egg of the two *Uria* species.

For this published paper, I conducted measurements and photographs of eggs (n = 991). I also performed all image processing pre-shape analysis, before conducting the automated shape analysis methods developed in **Chapter 2** and collating the dataset used in the study. Statistical analyses for the dwarf, normal and double-yolked egg comparisons presented in the paper were done by myself. I also contributed suggestions and improvements to the re-drafts of the manuscript.

Co-authors' contributions: T.R. Birkhead conceived the original idea and did the initial research for the article. T.R. Birkhead wrote the initial draft of the article and J.D. Biggins also subsequently contributed suggestions and approvements to the re-drafts of the manuscript. T.R. Birkhead assisted with the measurement of eggs. The majority of the statistical analyses and figures presented in the paper were done by J.D. Biggins.

J Ornithol (2017) 158:679–685
DOI 10.1007/s10336-017-1437-8

ORIGINAL ARTICLE

Egg shape in the Common Guillemot *Uria aalge* and Brunnich's Guillemot *U. lomvia*: not a rolling matter?

Tim R. Birkhead[1] · **Jamie E. Thompson**[1] · **John D. Biggins**[2]

Received: 21 September 2016 / Revised: 9 November 2016 / Accepted: 21 December 2016

Abstract The adaptive significance of avian egg shape is poorly understood, and has been studied only in those species producing pyriform (pear-shaped, or pointed) eggs: waders and guillemots (murres) *Uria* spp., albeit to a limited extent. In the latter, it is widely believed that the pyriform shape has evolved to minimise their likelihood of rolling off a cliff ledge: the idea being that the more pointed the egg, the narrower the arc in which it rolls, and the less likely it is it will fall from a cliff ledge. Previous research also claimed that the rolling trajectory—the diameter of the arc they describe—of Common Guillemot *U. aalge* eggs is influenced not only by its shape but also by its mass, with heavier (i.e. larger) eggs describing a wider arc than lighter eggs. The finding that both shape and mass determined the rolling trajectory of Common Guillemot eggs (the shape–mass hypothesis) was used to explain the apparent anomaly that Brünnich's Guillemot *U. lomvia* produce eggs that are less pointed, yet breed on narrower ledges than Common Guillemots. They are able to do this, it was suggested, because Brünnich's Guillemot eggs are smaller and lighter in mass than those of Common Guillemots. However, since some populations of Brünnich's Guillemots produce eggs that are as large or larger than those of some Common Guillemot populations, the shape–mass hypothesis predicts that that (1) larger (i.e. heavier) eggs of both guillemot species will be more pyriform (pointed) in shape, and (2) that eggs of the two species of same mass should be similarly pointed. We tested these predictions and found: (1) only a weak, positive association between egg volume and pointedness in both guillemot species (<3% of the variation in egg shape explained by egg volume), and (2) no evidence that eggs of the two species of similar mass were more similar in shape: regardless of their mass, Brunnich's Guillemot eggs were less pointed than Common Guillemot eggs. Overall, our results call into question the long-held belief that protection from rolling is the main selective factor driving guillemot egg shape.

Keywords Common Murre · Thick-billed Murre · Egg shape · Pyriform · Egg mass · Adaptive significance

Zusammenfassung

Die Eiform bei Trottel- und Dickschnabellumme (*Uria aalge, U. lomvia*): Wirklich ein Schutz vor dem Wegrollen?

Inwieweit die Form von Vogeleiern eine Anpassung darstellt, ist bislang kaum untersucht; am ehesten noch bei den Arten, die pyriforme bzw. spitzpolige Eier legen, nämlich Schnepfenvögel und Lummen (*Uria*-Arten). Im Fall der Lummeneier wird allgemein angenommen, dass die spitze Eiform als Schutz vor dem Wegrollen von Simsen bzw. Felsbändern entstanden ist: Je spitzer die Eier seien, um so enger der Bogen, den sie beim Rollen beschreiben. Das reduziere das Risiko, von schmalen

Communicated by F. Bairlein.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-017-1437-8) contains supplementary material, which is available to authorized users.

✉ Tim R. Birkhead
t.r.birkhead@sheffield.ac.uk

[1] Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

[2] School of Mathematics and Statistics, University of Sheffield, Sheffield S10 2TN, UK

Felsbändern herunterzufallen. Frühere Untersuchungen gingen davon aus, dass die Rollrichtung der Eier (d. h. der Durchmesser des Bogens, den die Eier beschreiben) bei Trottellummen (*U. aalge*) nicht nur von der Eiform, sondern auch von der Masse beeinflusst wird, wobei schwerere (also größere) Eier einen weiteren Bogen nehmen als leichtere. Die Tatsache, dass bei Trottellummen sowohl Form als auch Masse eines Eies die Rollrichtung vorgeben (die sog. Eiform- und Eimassenhypothese) wurde wiederholt bei der Diskussion der scheinbaren Regelabweichung herangezogen, dass Dickschnabellummen (*U. lomvia*) weniger spitze Eier als Trottellummen legen, obwohl sie auf noch schmaleren Felsbändern als letztere brüten. Dies sei deshalb möglich, weil die Eier von Dickschnabellummen kleiner und leichter als die von Trottellummen seien. Allerdings gibt es Populationen von Dickschnabellumme, die gleichgroße Eier wie Trottellummeneier oder sogar noch größere Eier legen. Die bereits erwähnte Eiform- und Eimassenhypothese sagt voraus, dass (1) die größeren (und damit schwereren) Eier beider Lummenarten eine spitzere Form haben und (2) gleich schwere Eier bei beiden Arten eine ähnlich spitze Form aufweisen sollten. Diese Voraussagen wurden von uns überprüft: (1) Es existiert eine schwache, positive Korrelation zwischen Eivolumen und Spitzpoligkeit bei beiden Lummenarten (weniger als 3% der Variation der Eiform werden vom Eivolumen erklärt). (2) Es gibt keine Evidenz, dass bei beiden Arten gleichschwere Eier eine höhere Formähnlichkeit aufweisen. Unabhängig von ihrer Masse waren Dickschnabellummeneier weniger spitz als Trottellummeneier. Damit stellen unsere Ergebnisse die langgehegte Vorstellung in Frage, dass ein Wegrollschutz den wichtigsten Selektionsfaktor bei der Entstehung der Eiform von Trottelllummen darstellt.

Introduction

The adaptive significance of avian egg shape is poorly understood (Barta and Székely 1997) and, except for those species producing pyriform (pear-shaped, or pointed) eggs such as waders and guillemots (murres) *Uria* spp., little studied. In waders, Andersson (1978) found that a pyriform egg allows females to maximise egg volume in a four-egg clutch while simultaneously maximizing the area in contact with the parents' brood patch during incubation. For the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*, the pyriform (pear-shaped) shape of their single egg has long been considered an adaption to minimise the risk of rolling off the narrow cliff ledges on which these species typically breed (MacGillivray 1852; Belopol'skii 1957; Del Hoyo et al. 1996; Gill 2007; reviewed in Birkhead 2016).

In support of this hypothesis, it has been shown that the guillemots' pyriform eggs tend to roll in an arc, whereas the 'elliptical-ovate' egg of the closely related Razorbill *Alca torda*—which breeds as pairs in cavities with little risk of the egg falling—rolls in a much wider arc (Belopol'skii 1957; Ingold 1980). Using plaster model eggs of different shapes, Tschanz et al. (1969) also showed that the more pointed the egg, the tighter the arc, and—presumably—the greater the protection conferred. However, Ingold (1980) subsequently showed that the plaster eggs used in Tschanz et al. (1969) study did not behave in the same the way as real eggs, and that, contrary to expectation, there was little difference in the rolling trajectories of real Common Guillemot and Razorbill eggs on natural substrates. Ingold (1980) concluded that: 'It has to remain unanswered whether the form of the guillemot egg [has] evolved in response to the pressure of the risk of falling off.' (translated from German).

Ingold (1980, 2016), however, has presented some evidence that the guillemot's pyriform egg still confers an advantage with respect to rolling. First, he found that, when comparing eggs of the same mass, the pyriform Common Guillemot eggs rolled in a slightly smaller arc than the elliptical-ovate Razorbill eggs ($n = 9$ for each species). Second, heavier (and thus larger) Common Guillemot eggs ($n = 9$) rolled in a wider arc than lighter eggs. Thus, the arc described by a rolling guillemot egg depends on both its shape and mass. Consequently, he argued that, because Common Guillemot eggs are larger (and therefore heavier) than Razorbill eggs, they would roll in an even wider arc and be especially vulnerable to falling if they were the same elliptical-ovate shape as Razorbill eggs.

Ingold (1980) further suggested that this interplay between shape and mass in determining an egg's rolling arc might also explain the anomaly that Brünnich's Guillemots produce eggs that are less pointed than those of Common Guillemots (Belopol'skii 1957; Harris and Birkhead 1985; Birkhead and Nettleship 1987b), even though Brünnich's Guillemots typically lay on narrower cliff ledges (Birkhead and Nettleship 1987a), and their eggs are therefore even more vulnerable to being lost by falling than Common Guillemot eggs. Ingold's (1980) explanation was that, because Brünnich's Guillemot eggs are smaller and lighter in mass than those of Common Guillemots', they can afford to be less pointed because lighter eggs roll in a smaller arc.

Ingold (1980) did not comment on the fact that some populations of Brünnich's Guillemots produce eggs that are as large or larger than those of some populations of Common Guillemot (e.g. Harris and Birkhead 1985). His hypothesis—that shape and mass together determine an egg's rolling trajectory—would therefore predict (1) that in both guillemot species, larger (i.e. heavier) eggs will be more pyriform or pointed in shape, and (2) that eggs of the two species of same mass should be pointed to a similar extent.

The aim of the present study was to test these two predictions, as an indirect test of the idea that the pyriform shape of guillemot eggs has evolved to minimise the risk of falling off cliff ledges.

Methods

Our measure of guillemot egg shape was the same as that used by Belopol'skii (1957) and Harris and Birkhead (1985): the proportion of overall egg length between the egg's widest point and its more pointed end. We call this measure 'pointedness', although Deeming and Ruta (2014) refer to it as the 'asymmetry ratio'. While there have been numerous efforts to characterise the shape of birds' eggs (see Deeming and Ruta 2014; Mityay et al. 2015 for further references), there is as yet no single parameter that adequately captures the degree to which eggs are pyriform in shape. We have not used Deeming and Ruta's (2014) principle component analyses to characterise shape in this present study because the principle component they use to describe shape (PC2) is closely correlated with our measure of pointedness (defined above).

We obtained pointedness measurements from photographs of eggs, taken under standardised conditions, from museum collections and from the field (see Online Resource 1, Sect. 1 for further details), and we additionally used these photographs to compute egg volume (see Online Resource 1, Sect. 1 for further details), which we used as a proxy for mass since the two variables [i.e. egg volume and egg mass (of both fresh and pipping eggs)] are highly correlated (Birkhead and Nettleship 1984). Specifically, for Common Guillemot fresh eggs: $r = 0.967$, $n = 37$; for pipping eggs, $r = 0.826$, $n = 86$; and for Brünnich's Guillemots fresh eggs: $r = 0.952$, $n = 78$; for pipping eggs, $r = 0.848$, $n = 66$; all $p < 0.001$ (Birkhead and Nettleship 1984: table VI). There was no difference in the density of eggs weighed within 24 h of laying between the two guillemot species (see Online Resource 1, Sect. 2).

Some populations of guillemots differ in both body size and absolute egg size (Harris and Birkhead 1985: pp. 168–174) and our original objective was to compare egg shape between and within populations of both *Uria* species. A simulation suggested that a sample of around 50 eggs from one population (colony) is needed to capture most of the variation in shape (results not shown); however, few museum collections had such large numbers of eggs from single locations. We therefore pooled samples for all locations for each species and compared the relationship between shape and volume and for each species separately. Only for Common Guillemots were there sufficient eggs (from three geographically distinct locations) to compare colonies: Skomer Island, Wales, UK, Bempton, Yorkshire, UK and Hjelmsoy (Hjelmsøya), Finnmark, Norway.

We also explored the relationship between egg shape and volume in more detail using a unique collection of eggs from a single colony (Bempton, Yorkshire, UK) that included unusually small ('dwarf') and unusually large ('doubled-yolked') eggs as well as 'normal' eggs (see Online Resource 1, Sect. 3 for further details).

Finally, we compared the shape of 78 eggs laid by 34 different females within and between years, to examine the consistency of shape within females (using the intraclass correlation coefficient; Lessells and Boag 1987; Nakagawa and Schielzeth 2010; see Online Resource 1, Sect. 4 for further details). Using eggs from Skomer Island, where we had measured and photographed both a haphazard sample of 210 eggs and 19 pairs of first and replacement eggs, we ran four different simulations of 100,000 replications each to compare the intraclass correlation between (1) random permutations of the replacement egg values, (2) a random selection of 19 eggs from other (i.e. non-replacement) Skomer eggs to pair with the first eggs, (3) 19 pairs drawn at random from other Skomer eggs, and (4) 19 pairs of eggs formed from other Skomer eggs, with the selection biased to mimic the approximately 5% volume difference observed (see Birkhead and Nettleship 1984) between first and replacement eggs.

Results

The rolling-in-an-arc hypothesis predicts that larger eggs of both guillemot species should be more pointed than smaller eggs. We tested this using data from 732 Common Guillemot eggs and 259 Brünnich's Guillemot eggs. Although pointedness increased significantly with egg volume, the slope of the relationship, which did not differ between the two species, was relatively shallow (Fig. 1). Moreover, egg volume explained just 0.5 and 2.7% of the variation in pointedness in the Common Guillemot and Brünnich's Guillemot, respectively (Fig. 1). This result provides only very weak support for the first hypothesis.

As previous studies have shown, the eggs of Brünnich's Guillemots are significantly less pointed than those of the Common Guillemot (e.g. Birkhead and Nettleship 1987b), but in our sample, there was no significant difference in mean egg volume between the two species (Fig. 1). Critically for Ingold's hypothesis, the eggs of Brünnich's Guillemot are less pointed than those of the Common

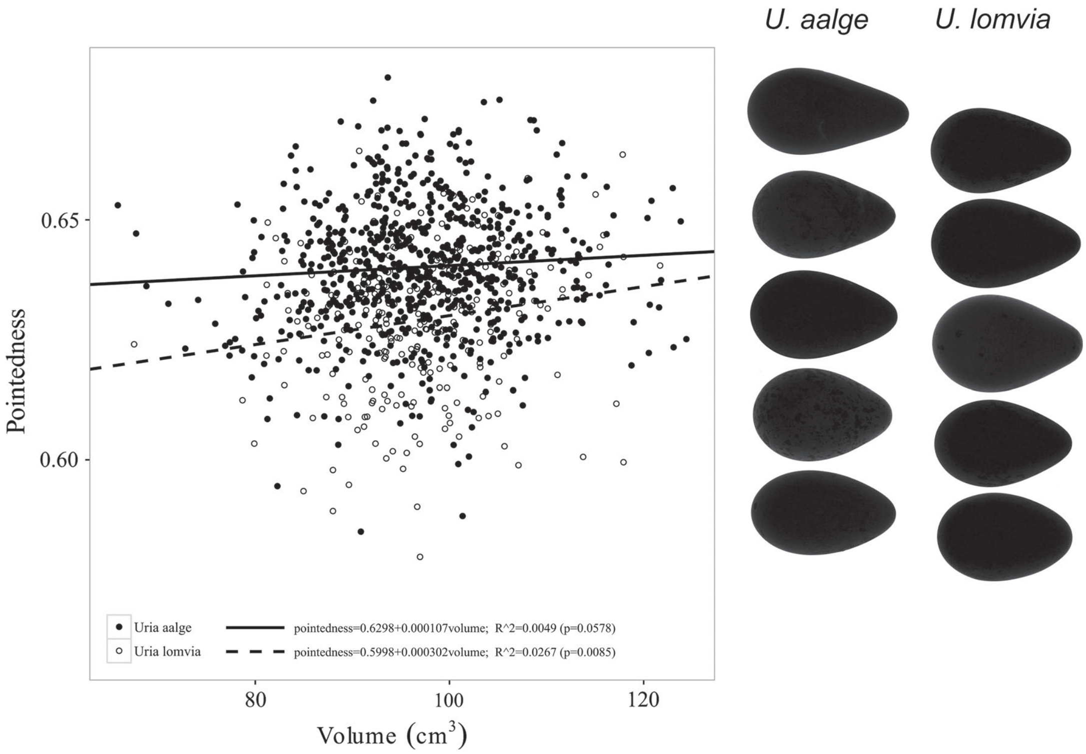


Fig. 1 Relationship between pointedness and egg volume (cm^3) for eggs of Common Guillemot *Uria aalge* (*filled circles*; $n = 732$) and Brünnich's Guillemot *U. lomvia* (*open circles*; $n = 259$). Using ANCOVA, the two slopes are not significantly different ($t = 1.603$, $df = 987$, $p = 0.109$) and, dropping this the interaction term, the common slope differs significantly from zero ($t = 2.963$, $df = 988$, $p = 0.0032$). Egg volume does not differ significantly between species (Welch's $t = 0.3364$, $df = 498$, $p = 0.74$); means: *U. aalge* 97.06, *U. lomvia* 96.86, 95% CI for difference (−0.96, 1.36). However, pointedness differed markedly between species (Welch's $t = 10.63$, $df = 420$, $p < 0.001$), with *U. aalge* eggs being more pointed; means: *U. aalge* 0.640, *U. lomvia* 0.629, 95% CI for difference (0.009, 0.013). On the *right* are examples of eggs (to scale, within the volume range 95–105 cm^3), of both species, representing the different values of pointedness, aligned with the *y* axis

Guillemot (Fig. 1) after controlling for egg volume, a result that also provides no support for the rolling-in-an-arc hypothesis.

A possible explanation for the slight increase in pointedness with volume is that the female's oviduct constrains the maximum egg diameter such that eggs that have a larger volume are longer by necessity. We explored this hypothesis in three ways. First, we looked at the relationship between volume and pointedness within colonies. This showed that, while the volume of Common Guillemot eggs differed significantly between the three geographic locations as expected (because of geographical differences in body mass; see Tuck 1961), shape did not (Fig. 2).

Second, comparing the shape of atypically small, atypically large eggs and 'normal' Common Guillemot eggs from a single colony, we found that large-volume, double-yolked eggs were significantly more pointed, and dwarf eggs significantly less pointed than 'normal' eggs (Fig. 3). This is consistent with the idea that egg volume plays a role in determining egg shape.

Third, comparing the shape of eggs laid by the same female, either within a season (first vs. replacement eggs) or between seasons (first eggs), we found high and significant repeatability in egg shape (between $r = 0.705$ and 0.921, for different datasets; all $p < 0.001$), demonstrating a strong female effect (see Online Resource 1, Sect. 4 for further details). For first and replacement eggs from Skomer, the intraclass correlation coefficient value was 0.825, a value that exceeded the maximum obtained in four different simulations (see "Methods") in every one of the 100,000 replicates per simulation ($p < 0.00001$).

Discussion

We found that egg volume (equivalent to mass) explained less than 3% of the variation in shape, and hence constitutes only very weak evidence for the hypothesis that larger (i.e. heavier) guillemot eggs are more pointed than lighter ones. In other words, since over 97% of the variation in egg shape is unexplained, size clearly has little effect on egg

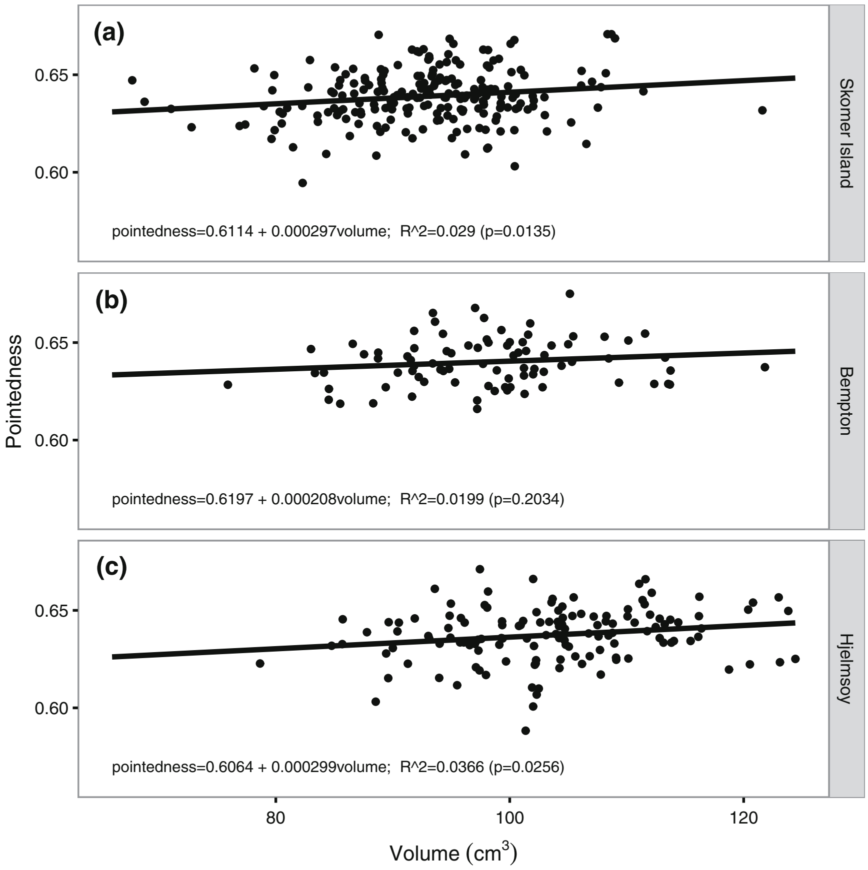


Fig. 2 Relationship between egg volume and pointedness of eggs from Common Guillemot *Uria aalge* populations at **a** Skomer Island, Wales ($n = 210$), **b** Bempton, Yorkshire, UK ($n = 83$), and **c** Hjelmsoy (Hjelmsøya), Finnmark, Norway ($n = 136$). The slopes do not differ significantly ($F_{(2,423)} = 0.11$, $p > 0.8$) and their common value differs significantly from zero ($t_{425} = 3.6$, $p < 0.001$), with 3.5% of the total variation in shape explained by egg volume. Pointedness does not differ significantly between colonies ($F_{(2,426)} = 1.16$, $p > 0.3$) but egg volume does ($F_{(2,426)} = 69.2$, $p < 0.0001$)

shape. A more plausible explanation for the slight positive relationship between volume and pointedness is that egg shape becomes slightly more pyriform as size increases as a result of some constraint on maximum egg diameter within the oviduct.

More critically, even after controlling for egg size, the eggs of Brünnich's Guillemot are less pointed than those of the Common Guillemot. Brünnich's Guillemots breed on much narrower ledges than Common Guillemots, and therefore if egg shape is an adaptation to facilitate rolling in an arc, we expect Brünnich's Guillemot eggs to be more pointed, not less, than those of Common Guillemots. Our result thus provides no support for the idea that guillemot egg shape is an adaptation to minimise the risk of rolling.

The factors influencing how the avian oviduct determines the shape of eggs are not well known. Egg shape is likely determined by the eggshell membrane before the shell is formed, and that membrane is formed within the isthmus region of the oviduct. It is assumed that one end of this region is more constricted as the membrane is being formed (Bradfield 1951; Smart 1991). In addition, it is known that egg length and breadth (diameter) in particular are consistent within female birds (Romanoff and Romanoff 1949), including guillemots and the Razorbill (Birkhead and Nettleship 1984). Here, we show that egg shape within females, at least for Common Guillemots, is also repeatable, although the reasons for this are unknown.

It is striking that, with very few exceptions, almost all previous researchers have attempted to explain the pyriform shape of guillemot eggs as an adaptation to minimise the risk of rolling (Belopol'skii 1957; Tschanz et al. 1969; Ingold 1980). This narrow focus may be a consequence of the way guillemot colonies were studied and exploited during most of the twentieth century. In the past, those collecting eggs or studying guillemots typically climbed onto breeding ledges causing the incubating birds to depart in panic, and many of their eggs rolled off the ledge (Belopol'skii 1957; Uspenski 1956; Tuck 1961). Some studies even looked at the effect of gunshots, which caused an immediate mass departure of incubating birds in panic and a concomitant loss of eggs (Belopol'skii 1957). All this suggested that egg loss through rolling must be a major mortality factor for breeding guillemots. More recent observational studies of undisturbed guillemots showed that it is relatively rare for an egg to roll off a ledge (Birkhead 1977; Harris and Wanless 1988). Unless disturbed by large terrestrial predators such as man, guillemots of both species rarely leave their egg unattended: one

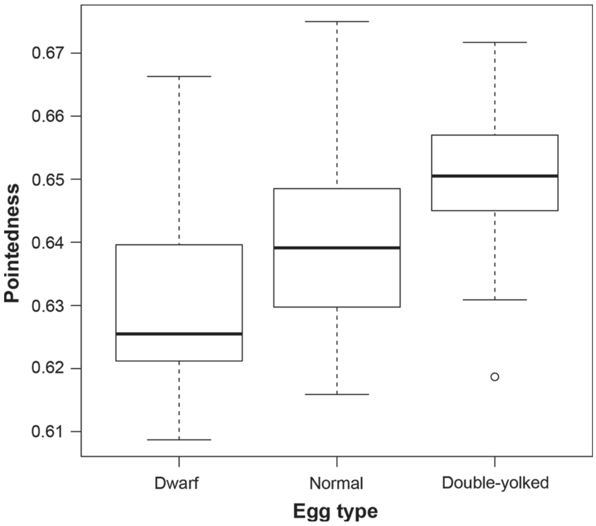


Fig. 3 Variation in pointedness for Common Guillemot *Uria aalge* dwarf eggs ($n = 13$; mean egg volume $\mathrm{cm}^3 \pm 95\%$ CL: 58.49 ± 2.58), normal eggs ($n = 83$; 97.95 ± 1.79) and double-yolked eggs ($n = 37$; 142.40 ± 2.41) previously collected from a single colony found at Bempton, Yorkshire, UK. Pointedness (mean ± 95% CL): dwarf $= 0.631 \pm 0.009$; normal $= 0.640 \pm 0.003$, and double-yolked $= 0.650 \pm 0.003$, (ANOVA $F_{(2,130)} = 14.86$, $p < 0.0001$; Tukey posthoc comparisons: dwarf vs. double yolk ($p < 0.001$); normal vs. double yolk ($p < 0.001$); normal vs. dwarf ($p < 0.05$)). *Boxes* are the interquartile range, *black line* within the box is the median, the *whiskers* show the highest and lowest values and *open circles* indicate potential outliers

partner incubates continuously. Escaping from predators that threaten their own life and abandoning their egg is exactly what we might expect from a long-lived species like guillemots.

Ingold's (1980, 2016) conclusion that both shape and mass affect an egg's rolling trajectory is based on a rather small sample size ($n = 9$ Common Guillemot and $n = 9$ Razorbill eggs). Also, as we show in this present study, eggs of the same volume or mass can vary considerably in shape (Fig. 1), but Ingold provides no information on egg shape, nor does he tell us whether he even matched eggs of similar mass in his rolling experiments. Third, as had been shown previously and confirmed by his own studies, egg mass declines during the course of incubation, yet he does not state that the eggs used in these experiments were at the same stage of incubation. With at least three different factors affecting an egg's rolling trajectory, Ingold's (1980) sample size of 9 is almost certainly too low to draw any firm conclusions.

Ingold (1980) acknowledged that other selection pressures, such as 'weather conditions, predators and conspecifics', might explain the pyriform shape of the Common Guillemot's egg, but he did not elaborate nor test any other hypotheses. He also showed that parental behavior, including keeping the egg between their legs with the blunt end directed away from the bird, was important in keeping the egg on the ledge (Ingold 1980; see also Tschanz 1990; Ingold 2016). Elsewhere, we consider several other hypotheses for the pyriform shape of guillemot eggs (Birkhead et al. 2017).

Acknowledgements TRB conceived the project. TRB and JET collected the data; JET and JDB analysed the data; and TRB wrote the manuscript. We thank the following museum curators for allowing us to examine their eggs: Jean Woods (Delaware Natural History Museum, USA), Douglas Russell (Natural History Museum at Tring, UK), Rob Barrett (Tromsø Zoology Museum, Norway), Henry McGhie, (Manchester University Museum, UK), Brian Schmidt (Smithsonian Institute Washington, US), Jon Fjeldsa (Natural History Museum of Denmark), Ingvar Byrkjedal (University Museum of Bergen, Norway), Julian Carter (National Museum of Wales, UK) and Dan Gordon (Tyne and Wear Archives and Museums, UK). Mark Hipfner kindly provided the data that allowed us to calculate the density of fresh guillemot eggs. The translation of Ingold (1980) was made by Claudius Kerth. We thank Nicola Hemmings, Paul Ingold, Duncan Jackson, Bob Montgomerie, Julie Riordan, Tony Ryan and Karl Schulze-Hagen for valuable discussion. Thanks also to The Wildlife Trust of South and West Wales for permission to work on Skomer Island, and to the wardens there (Birgitta Büche and Edward Stubbings) for their help. We are grateful to Duncan Jackson and Bob Montgomerie for comments on the manuscript. The study was funded in part by a grant (to TRB) from the Leverhulme Trust, to whom we are very grateful. This work was carried out in compliance with the current laws in the United Kingdom.

References

Andersson M (1978) Optimal egg shape in waders. Ornis Fenn 55:105–109

Barta Z, Székely T (1997) The optimal shape of Avian eggs. Funct Ecol 11:656–662

Belopol'skii LO (1957) Ecology of sea colony birds of the Barents Sea. Israel Program for Scientific Translations, Jerusalem (Translated from Russian 1961)

Birkhead TR (1977) The effect of habitat and density on breeding success in the Common Guillemot *Uria aalge*. J Anim Ecol. 46:751–764

Birkhead TR (2016) The most perfect thing: the inside (and outside) of a bird's egg. Bloomsbury, London

Birkhead TR, Nettleship DN (1984) Egg size, composition and offspring quality in some Alcidae (Aves: charadriiformes). J Zool Lond 202:177–194

Birkhead TR, Nettleship DN (1987a) Ecological relationships between Common Murres, *Uria aalge* and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. II: breeding success and site characteristics. Can J Zool 65:1630–1637

Birkhead TR, Nettleship DN (1987b) Ecological relationships between Common Murres, *Uria aalge* and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. I: morphometrics and timing of breeding. Can J Zool 65:1621–1629

Birkhead TR, Thompson JE, Jackson D, Biggins JD (2017) The point of a guillemot's egg. Ibis. doi:10.1111/ibi.12458

Bradfield JRG (1951) Radiographic studies on the formation of the hen's eggshell. J Exp Biol 28:125–140

Deeming DC, Ruta M (2014) Egg shape changes at the theropod-bird transition, and a morphometric study of amniote eggs. R Sci Open Sci. doi:10.1098/rsos.140311

Del Hoyo J, Elliot A, Sartgatal J (1996) Handbook of the birds of the world, vol 3. Lynx, Barcelona

Gill F (2007) Ornithology. Freeman, New York

Harris MP, Birkhead TR (1985) Breeding ecology of the Atlantic Alcidae. In: Nettleship DN, Birkhead TR (eds) The Atlantic Alcidae. Academic, London, pp 155–205

Harris MP, Wanless S (1988) The breeding biology of guillemots Una aalge on the Isle of May over a six year period. Ibis 130:172–192

Hewitson WC (1831) British Oology: being illustrations of the eggs of British birds. Empson, Newcastle upon Tyne

Ingold P (1980) Anpassungen der Eier und des Brutverhaltens von Trottelummen an das Brüten auf felssimen. Z Tierpyschol 53:341–388

Ingold P (2016) Brüten an Felsklippen—was Trottellummen (*Uria aalge* ualgebefühigt, auf Felssimsen und in dichten Gemeinschaftenzu brüten. Orn Beob 113:85–120

Lessells CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. Auk 104:116–121

MacGillivray W (1852) A History of British Birds. Scott, Webster and Geary, London

Mityay IS, Matsyura AV, Jankowksi K (2015) Application of bird egg morphometrics in phylogeny. Acta Biol Sib 1:92–102

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev 85:935–956

Romanoff AJ, Romanoff AL (1949) The avian egg. Wiley, New York

Smart IHM (1991) Egg-shape in birds. In: Deeming DC, Ferguson MJW (eds) Egg incubation: its effects on embryonic development in birds and reptiles. Cambridge University Press, Cambridge, pp 101–116

Tschanz B (1990) Adaptations for breeding in Atlantic Alcids. Neth J Zool 40:688–710

Tschanz B, Ingold P, Lengacher H (1969) Eiform und Bruterfolg bei Trottellummen. Ornithol Beob 66:25–42

Tuck LM (1961) The Murres: their distribution, populations and biology—a study of the genus *Uria*. Can Wildl Monogr Ser 1:260

Uspenski SM (1956) Bird bazaars of Novaya Zemlya. Canadian Wildlife Service translations of Russian game reports, vol 4. CWS, Ottawa (Translated from Russian 1958)

CHAPTER 5:

The point of a Guillemot’s egg

The point of a Guillemot's egg

Birkhead, T. R., Thompson, J. E., Jackson, D. and Biggins, J. D. (2017). *Ibis*, **159**, 255-265.

Original article and Supplementary Materials can be found using the link below:

https://onlinelibrary.wiley.com/doi/full/10.1111/ibi.12458

Chapter context and thesis author's contributions: Considering that Chapter 4 presents published work that provides evidence that brings into question the validity of the 'rolling-in-an-arc' adaptive explanation for the Common Guillemot's pyriform egg shape, this chapter presents a published article in Ibis that proposes and examines two novel adaptive hypothesis for this extreme egg shape. These adaptive hypotheses are: [1] prevention and/or limitation of mechanical damage during incubation in typically highly dense breeding colonies, and [2] the limitation of faecal/debris contamination effects on egg function during incubation on guano-covered breeding ledges. The published paper begins to examine the plausibility of these novel adaptive explanations for the Common Guillemot's pyriform egg shape and presents some initial evidence for these.

For this published work, contact index measurements presented were obtained from automated image analysis software conducted by myself. The faecal/debris contamination hypothesis was in part developed by myself, from direct observations on the breeding ledges of Common Guillemots. Colour photographs for measuring faecal contamination on Common Guillemot and Razorbill eggs were taken in-situ by myself under licenced permission from Natural Resources Wales. Measurement of egg photographs for faecal contamination was done and collated by myself and I, in part, assisted with the statistical analyses and producing of the figures for this data. I also provided assistance with improvements to the re-drafts of the manuscript.

Co-authors' contributions: T.R. Birkhead conceived the overall project and conducted the initial research for this manuscript. T.R. Birkhead wrote the original manuscript and developed and improved the re-drafts, along with contributions from D. Jackson and J.D. Biggins. The prevention of mechanical damage hypothesis was developed by T.R. Birkhead. J.D. Biggins developed the automated image analysis software that obtained the contact index measurements. The faecal/debris contamination hypothesis was, in part, developed by T.R. Birkhead. T.R. Birkhead assisted with collecting eggs for faecal/debris contamination measurement sampling. D. Jackson assisted with the faecal/debris contamination statistical analyses presented in the paper. All porosity and eggshell thickness measurements, statistical analyses and figures were done by D. Jackson.

IBIS
BOU international journal of avian science

Ibis (2017), **159**, 255–265
doi: 10.1111/ibi.12458

The point of a Guillemot's egg

TIM R. BIRKHEAD,[1]* JAMIE E. THOMPSON,[1] DUNCAN JACKSON[1] & JOHN D. BIGGINS[2]
[1] *Department of Animal & Plant Sciences, University of Sheffield, Sheffield, UK*
[2] *School of Mathematics and Statistics, University of Sheffield, Sheffield, UK*

The adaptive significance of avian egg shape in birds is poorly understood. The pyriform (pear-like) shape of the Common Guillemot's *Uria aalge* egg has long been considered to be an adaptation to prevent eggs rolling off the bare cliff ledges on which this species breeds. Rolling was thought to be prevented either by the egg spinning like a top, which is not the case, or by rolling in an arc, which it does but with little influence on whether the egg will fall from a ledge. We therefore sought alternative explanations for the pyriform shape of the Common Guillemot's egg. This species breeds in extremely dense colonies, which makes their eggs vulnerable to mechanical damage from conspecifics, and to contamination by debris such as faeces and soil. We present evidence consistent with both these possible explanations. First, the pyriform shape of Common Guillemot eggs means that a higher proportion of the eggshell lies in contact with the substrate and this may minimize the effect of impacts. Resistance to impacts may be further enhanced because their eggshells are especially thick where they are in contact with the substrate. Secondly, Common Guillemot eggs are often heavily contaminated with faecal material and other debris during incubation. Most contamination is on the pointed end of the egg where it is in contact with the substrate; the pyriform shape thus keeps the blunt end of the egg, which has the highest porosity, relatively free of contamination, which in turn may facilitate both gas exchange during incubation and the hatching process, because the chick emerges from the blunt end of the egg.

Keywords: Common Murre *Uria aalge*, egg shape, eggshell thickness, faecal contamination, pyriform, Razorbill *Alca torda*, stress concentration.

The shape of birds' eggs varies considerably, from near-spherical, to oval, elongate, bi-conical and pyriform (Thomson 1964). With few exceptions (e.g. in waders, Andersson 1978), the adaptive significance of avian egg shape is poorly understood. However, the pyriform (pear-shaped) egg of the Common Guillemot *Uria aalge* (hereafter Guillemot) and Brünnich's Guillemot *Uria lomvia* has long been considered an adaptation to reduce the risk of rolling off the narrow, rocky cliff ledges on which these species breed without constructing a nest (MacGillivray 1852, Belopol'skii 1957, Gill 2007).

The first explanation for the Guillemot's pyriform egg shape was that it allowed the egg to spin like a top (on its side) when knocked or blown by the wind (Hewitson 1831). However, the ability of Guillemot eggs to spin was based on empty museum eggshells and is biologically meaningless, and it was later shown that intact Guillemot eggs containing yolk and/or an embryo did not move in this way when knocked. Instead, they tend to roll in an arc (Belopol'skii 1957, Ingold 1980, Birkhead 2016). In contrast, the 'elliptical ovate' (i.e. much less pointed) egg of the Razorbill *Alca torda* rolls in a much wider arc (Kaftanovski 1941, Belopol'skii 1957, Ingold 1980).

Tschanz *et al.* (1969) provided what appeared to be clear-cut evidence that as the shape of Guillemot eggs becomes more pyriform, the tighter the rolling arc becomes and the greater the protection it provides against falling off a ledge. However, Tschanz *et al.*'s (1969) results were

*Corresponding author.
Email: t.r.birkhead@sheffield.ac.uk

derived from model eggs made of plaster, which do not behave in the same way as real eggs (Ingold 1980). Comparing real Guillemot and Razorbill eggs on natural substrates, Ingold (1980) found little difference in their rolling arcs, suggesting that the pyriform shape of the Guillemot's egg provides little or no protection from rolling. Even so, and slightly confusingly, having found that mass as well as shape affected an egg's rolling trajectory, Ingold (1980) concluded that a pyriform shape must still be advantageous for Guillemot eggs, because if they were the same shape as Razorbill eggs (which are smaller and therefore lighter in mass), they would be more likely to roll off the ledge.

The evidence that the Guillemot's pyriform egg shape is an adaptation to facilitate rolling in an arc, thus reducing the risk of rolling off the ledge, is very limited. Moreover, there are several reasons for questioning the assumptions of the rolling-in-an-arc hypothesis: (1) Guillemots often breed on ledges much narrower than the arc described by a rolling egg (Harris & Birkhead 1985, Birkhead & Nettleship 1987); (2) as Guillemots typically incubate facing the cliff wall with the pointed end of their egg directed towards the cliff edge (Tschanz 1968, T.R. Birkhead pers. obs.), a dislodged egg would roll *outwards* towards the cliff edge and thus be more likely to fall; (3) Guillemot eggs vary considerably in shape (Tschanz *et al.* 1969, Birkhead *et al.* 2017), suggesting that there is little stabilizing selection on egg shape; (4) Brünnich's Guillemots produce eggs that are less pyriform-shaped than those of Common Guillemots (Belopol'skii 1957, Harris & Birkhead 1985), despite their breeding on narrower ledges (Birkhead & Nettleship 1987). Ingold (1980) explained this apparent anomaly by invoking the interaction between shape and mass and suggesting that because the eggs of Brünnich's Guillemots were smaller and lighter in mass, they would roll in a smaller arc and thus be less vulnerable to falling than are Common Guillemot eggs. However, a test of this hypothesis comprising a comparison of the shape and mass of Common and Brünnich's Guillemot eggs provided no support for this idea (Birkhead *et al.* 2017).

The eggs of both guillemot species are subject to two selection pressures that have not previously been considered: the risk of physical damage from conspecifics and contamination by debris.

Guillemots typically breed in direct bodily contact with conspecifics at high densities (regularly at around 20 pairs per square metre, but up to 70 pairs per square metre; Birkhead 1993) on both broad and narrow ledges (Birkhead 1977). Incubating birds are frequently jostled by their neighbours during fights and it is not uncommon for birds returning from the sea to land heavily (body mass *c.* 1 kg) directly on top of incubating conspecifics. It has been argued that, all else being equal, a spherical egg will have the greatest resilience to impacts (Smart 1969, Bain 1991). However, no bird lays a completely spherical egg. Moreover, with a spherical egg, the effects of any impact, from above, for example, would be concentrated onto a very small region of the shell where the egg is in contact with the substrate. In engineering terms, this point is referred to as the 'stress concentration' (Pilkey & Pilkey 2008) and is the place on the shell where it is most likely to break. With a pyriform egg, it seems plausible that a greater proportion of the shell lies in contact with the substrate, meaning that the stress of any impact will be spread over a greater surface area, thereby conferring greater eggshell strength.

Guillemots defecate without regard to their neighbours, so that the rocky substrate on which they breed is usually covered with faecal material. Along with any soil already present at the breeding site, faecal material can contaminate the eggs, especially in wet weather. Brünnich's Guillemots breed under similar crowded and 'dirty' conditions, albeit on narrower cliff ledges at lower density (Gaston & Nettleship 1981, Birkhead & Nettleship 1987). Contamination of the eggshell by faeces and other debris can potentially compromise gas exchange and facilitate microbial infection, both of which can be fatal to avian embryos (Board 1982, Verbeek 1984).

Our aim here is to offer two new explanations for the pyriform shape of Guillemot eggs: first, the pyriform egg shape confers physical strength that enables Guillemot eggs to withstand impacts resulting from the vigorous 'rough and tumble' of a dense breeding colony; secondly, the pyriform egg shape reduces the consequences of debris contamination of the egg surface. We provide data in support of each possibility, and offer some suggestions for further study.

METHODS

To obtain measurements of eggshell characteristics we used Guillemot eggs from our field site at

Skomer Island, Wales, UK (under licence). We made some comparisons between the eggshells of Guillemots and Razorbills, the latter also from Skomer and collected under licence; all eggs were from 2014, 2015 and 2016. The Razorbill is closely related to the Guillemot and also breeds colonially on sea cliffs (and often in close proximity to Guillemots), but as isolated pairs and often in rocky cavities where there is little risk of their egg falling (Harris & Birkhead 1985, Smith & Clarke 2015). Ingold's (1980) investigation of the adaptive significance of Guillemot egg shape was based partly on comparisons with Razorbill eggs, which is why we have included data for that species here.

Contact of the eggshell with the substrate

We calculated the 'contact index' (defined below) for Guillemot and Razorbill eggs to quantify the extent to which the eggshell is in contact with the substrate and the extent to which the pyriform shape of the Guillemot egg results in a higher value. A greater area in contact with the substrate would reduce the stress per unit area should there be an impact, particularly from above, and thus reduce the probability of breakage. To obtain a sufficiently large sample of eggs of both Guillemot (n = 83) and Razorbill (n = 79) from the same colony, we used eggshells collected from Bempton, Yorkshire, UK, and held in the Natural History Museum, Tring, UK, for this part of the study.

Typically, an egg's centre of gravity moves towards the pointed end of the egg as incubation proceeds and the air cell increases in size, changing the egg area in contact with the substrate over incubation (Belopol'skii 1957). Because Guillemots incubate in a semi-upright posture, the weight of the bird's body essentially causes the egg to adopt the maximum contact with the substrate (Tschanz 1990, T.R. Birkhead pers. obs.). To account for this, we used the following method to obtain an objective index of the maximum proportion of the egg in contact with the substrate during incubation. Using the outline from an egg silhouette image obtained by photographing each egg against a lightbox, we mathematically captured the shape of an egg from which we could derive the other parameters including the two-dimensional area of the silhouette and the egg surface area, using the methods described by Preston (1953) and Todd and Smart (1984). The formula for the shape was then used to locate the place on the eggshell surface where the profile was flattest. Although the actual profile is a smooth curve with only a tiny point of contact, in reality imperfections in the egg surface and irregularities in the substrate will spread this contact. In the plane that is tangential at the point where the profile is flattest, we calculated the area within 0.2 mm of the egg surface on the assumption that a 0.2-mm tolerance reflects both the flexing of the shell and these imperfections and irregularities. That area in contact with the substrate was then expressed as a percentage of the area of the egg silhouette, so that egg size is not a factor, to give the 'contact index'. We also explored the consequences of tolerances of 0.1 and 0.5 mm to account for the unevenness of the substrate. See Appendix S1 for further methodological details.

Measuring eggshell thickness

Eggshell strength is determined in part by thickness (Romanoff & Romanoff 1949), and as the two *Uria* species have thicker eggshells than those of any other bird laying similarly sized eggs (Schoenwetter 1960–1992, see also Pirie-Hay & Bond 2014), it follows that their eggshells are particularly strong. Our aim was to compare shell thickness in different regions of the eggshell, to establish whether the shell was thickest in the region where it is in contact with the substrate. Different studies have measured eggshell thickness in different ways, but most have assessed the entire thickness of the shell, with or without the shell membrane. According to Bain (2005), however, the measure of thickness that best reflects eggshell strength is the distance between the point of fusion of the palisade columns to the outer edge of the shell accessory material; this measure is referred to as 'effective thickness' (Fig. S2 and Table S1).

Eggshell thickness measures were obtained from 10 Guillemot eggs collected on Skomer Island in 2014 (n = 5), 2015 (n = 3) and 2016 (n = 2). For each egg, 10 measures were taken from the blunt pole, the equator (maximum diameter) and near (but not at) the pointed end of the egg (see Results for details on sampling location) using micro-CT scanning. From these 10 measures, we calculated mean values for several different measures of thickness for each eggshell fragment, obtained as follows.

Fresh eggs were drained of their contents, washed in distilled water and allowed to dry. To obtain shell fragments for measuring, a hand-held rotary saw (DREMEL Multi, Mod. 395 Type 5 Code 83; DREMEL, USA) was used to cut *c.* 1-cm^2 pieces from each of three regions of the egg. Eggshell fragments were scanned in a Bruker Skyscan 1172 using the following settings: scanner set at 100 kV electron acceleration energy and 90 μA current with the sample 48.7 mm from the X-ray source with a 1.0-mm aluminium filter, with the sample 283.349 mm away from the camera. Camera resolution was set at 1048 × 2000 pixels, with a pixel size of 4 μm. We used the same setting for each scan, collecting a total of 1048 projection images using a rotation step size of 0.4° and a detector exposure of 1475 ms integrated over three averaged images resulting in a total scan time of 50 min. Two eggshell fragments were scanned during each session. Projection images were then reconstructed in NRECON software (version 1.6.10.1) before image analysis was performed in CT analyser (CTAN, version 1.14.41), CTVOX (version 3.0; all the above software provided by Bruker micro-CT, Kontich, Belgium) and IMAGEJ (version 1.49p; Schneider *et al.* 2012). Reconstruction parameters were: dynamic image range; minimum attenuation coefficient = 0, maximum = 0.08, level 2 Gaussian smoothing, ring artefact correction = 12, beam hardening correction of 20% and auto misalignment compensation, images saved as 8-bit bitmaps. Shell thickness was measured in CTAN software using the line measurement tool at 10 haphazardly selected locations within each shell fragment.

To test for differences in eggshell thickness between the three regions of the Guillemot eggshell we ran a one-way ANOVA, using repeated measures analysis to control for multiple measures from the same egg. To test for differences in the relative variation in effective eggshell thickness between Guillemot and Razorbill eggs (whose eggs are slightly smaller: Harris & Birkhead 1985), we calculated the ratios between eggshell thickness in different regions of the eggs (blunt/equator, blunt/point and equator/point) of both species.

Measuring debris contamination on the egg surface

We recorded the extent of debris (mainly faeces and soil) contamination of 59 Guillemot and 40 Razorbill eggs on Skomer Island, Wales, in 2016. To standardize the time period available to accumulate debris, we photographed eggs on a single occasion 22–25 days after each species' median laying date (9 May for Guillemots and 12 May for Razorbills; T.R. Birkhead pers. obs.). The eggs of both species were all from the same (mixed) colony where the two species were breeding as close as 15 cm to each other.

Using a life-size image of each egg, we superimposed a grid of 5-mm squares, and recorded whether each egg had any opaque debris (i.e. debris that obscured the ground colour or maculation), to provide an estimate of the proportion of 'dirty' eggs. We also recorded whether each 5-mm square contained any debris, to provide an estimate of the extent (expressed as a percentage) of the total area of the blunt end (i.e. lying above the maximum egg diameter) and the pointed end (below the maximum egg diameter) of each egg that was covered by debris. To check for repeatability (Lessells & Boag 1987, Nakagawa & Schielzeth 2010), 20 Guillemot and Razorbill egg images were scored independently by five different individuals; repeatability was found to be high (blunt end: $F_{19,80} = 62.3$, $r = 0.92$, $P < 0.0001$; pointed end: $F_{19,80} = 43.8$, $r = 0.89$, $P < 0.0001$).

Measuring eggshell porosity

The efficacy of gas exchange between the embryo and outside world is determined by the number and dimensions of the eggshell pores (Ar & Rahn 1985). Gas exchange is likely to be compromised if eggshell pores are blocked with debris (Board 1982).

The limiting dimension for the diffusion of gases is the minimum cross-sectional pore area, that is, the narrowest part of the pore (Tøien *et al.* 1988). Using *c.* 1-cm^2 fragments of eggshell from three different regions of each egg (as above), we calculated eggshell porosity (i.e. total pore area in mm^2) by multiplying the average minimum cross-sectional area of pores by the pore density (pores per mm^2), to give the total functional pore area in 1 mm^2 of eggshell (Ar & Rahn 1985). Our method was similar to that of Riley *et al.* (2014), who also used micro-CT to identify and measure the narrowest cross-sectional pore areas directly. Fragment area and minimum cross-sectional pore area were both measured in IMAGEJ. Pores were measured by re-slicing the reconstructed image stack and taking measurements from orthogonal views, working through 4-μm image slices one at a time from the shell outer surface to the inner surface until the minimum cross-sectional area of the pore was measured. Ten pores per fragment were haphazardly selected for measurements. Image stacks were then loaded into CTVOX to produce 3-D volumetric reconstructions of the eggshell fragment, and the number of pores was counted and then divided by fragment area (mm^2) to obtain pore density.

We determined the repeatability of porosity and shell thickness measures within each region of an egg using three fragments from each region of five Guillemot and five Razorbill eggs (Lessells & Boag 1987, Nakagawa & Schielzeth 2010). Repeatability was very high for effective shell thickness for both species ($r = 0.97$, for both species) and reasonably high for porosity (Guillemot: $r = 0.74$, Razorbill: $r = 0.58$) (Table S2).

To test for differences in porosity between the three regions of the Guillemot eggshell, we ran a one-way ANOVA on log-transformed data, with the repeated measures analysis to control for multiple measures for each egg. Log transformation was necessary to make the Guillemot egg data fulfil the assumptions of the analysis. This was not necessary for the Razorbill egg data.

All data were analysed using the base package R (R Development Core Team 2012). Where two-sample t-tests were used, Welch's correction was applied to account for unequal sample sizes and variances and thus provide degrees of freedom that are lower than would otherwise be expected for given samples sizes. Means are expressed ± 1 sd.

RESULTS

Contact of the eggshell with the substrate

The Guillemot's pyriform-shaped egg is characterized by a relatively long, straight surface below the equator towards the point, compared with that of the elliptical-ovate egg of a Razorbill (Fig. 1). The contact index of Guillemot eggs, assuming a tolerance of 0.2 mm, was significantly greater (mean = 2.14 ± 0.32, $n = 83$) than that of Razorbill eggs (mean = 1.81 ± 0.14, $n = 79$) (Welch's two-sample t-test: $t = 8.48$, df = 111, $P < 0.001$; Fig. 1). We obtained very similar results with tolerances of 0.1 and 0.5 mm, both of which were highly correlated with the 0.2-mm tolerance measures (Spearman's correlation: $r_s > 0.997$ in both cases). For 83 Guillemot eggs, this contact index is strongly and positively correlated (Spearman's correlation: $r_s = 0.83$, $n = 83$, $P < 0.001$) with the degree of pointedness (i.e. the proportion of overall egg length between the egg's widest point and the more pointed end of the egg). These results are consistent with our hypothesis that the pyriform shape of the Guillemot's egg results in a relatively larger proportion of the egg's surface being in contact with the substrate, potentially reducing the stress per unit area during impacts.

Eggshell thickness

Guillemot eggshells were thinnest (total eggshell thickness including the shell membranes) at the blunt end (536 μm ± 23.8) and thickest at the equator (651 μm ± 28.2) and pointed end (639 μm ± 39.5). This difference in thickness between the blunt end and the other regions was significant ($F_{2,18} = 44.1$, $P < 0.001$; Tukey multiple comparison test: $P < 0.05$). Pirie-Hay and Bond (2014) obtained a similar result with Common Guillemot eggs, as did Uspenski (1958) for

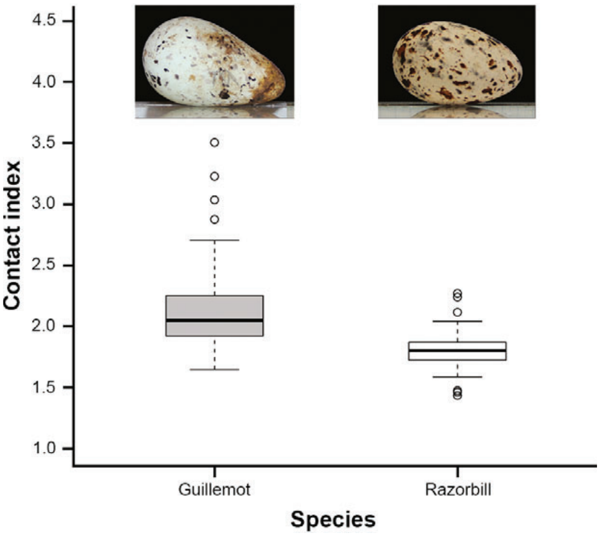


Figure 1. Contact index in Guillemot ($n = 83$) and Razorbill eggs ($n = 79$): museum specimens collected from Bempton Cliffs, Yorkshire, UK. Upper images show profiles of an intact and partly incubated Guillemot egg (left) and Razorbill egg (right), to illustrate the difference in the percentage of eggshell in contact with the substrate. Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values and open circles indicate potential outliers. The contact index of Guillemot eggs is significantly greater than that of Razorbill eggs ($P < 0.001$): see text for details. [Colour figure can be viewed at http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1474-919X]

Brünnich's Guillemot eggs. In terms of effective eggshell thickness (see Methods), the equator was significantly thickest (471 μm ± 23.8), followed closely by the pointed end (432 μm ± 30.6), and the blunt end of eggs was thinnest (362 μm ± 32) ($F_{2,18} = 41.0$, $P < 0.001$; Tukey multiple comparison test: $P < 0.05$). However, effective thickness ratios between different regions of the egg showed that the pattern in shell thickness differs between Guillemot and Razorbill eggs, primarily in the magnitude of difference between the blunt and equator region, but also in the magnitude of difference between the equator and pointed region (Fig. 2).

Debris contamination on the egg surface

Guillemot eggs were significantly more likely to have any visible faecal material and/or soil – measured as opaque contamination – on their surface (56/59, 97%) than were Razorbill eggs (17/40, 43%) ($\chi^2 = 31.2$, df = 1, $P < 0.001$; Fig. 3). In the Guillemot eggs, debris contamination was more frequent on the pointed end of the egg than on the blunt end (paired *t*-test: $t = 7.75$, df = 58, $P < 0.001$), but this was not the case with the Razorbill eggs (paired *t*-test: $t = 0.01$, df = 39, $P = 0.992$) (Fig. 4).

Eggshell porosity

The blunt end of Guillemot eggshells was significantly more porous than other egg regions (one-way ANOVA with repeated measures: $F_{2,8} = 13.5$, $P < 0.001$; Tukey multiple comparison test: $P < 0.05$; Fig. 5). Specifically, the blunt end of a Guillemot egg ($3.21 \times 10^{-4} \pm 1.58 \times 10^{-4}$ mm^2) was significantly more porous than both the equator ($1.24 \times 10^{-4} \pm 7.25 \times 10^{-5}$ mm^2) and the pointed region ($9.68 \times 10^{-5} \pm 4.57 \times 10^{-5}$ mm^2). Although the pattern was similar in Razorbill eggs, it was much less pronounced and not statistically significant (one-way ANOVA with repeated measures: $F_{2,8} = 3.13$, $P = 0.0684$; Fig. 5).

DISCUSSION

Contrary to popular belief, there is almost no evidence that the pyriform shape of Guillemot eggs, and their resulting tendency to roll in an arc, is an

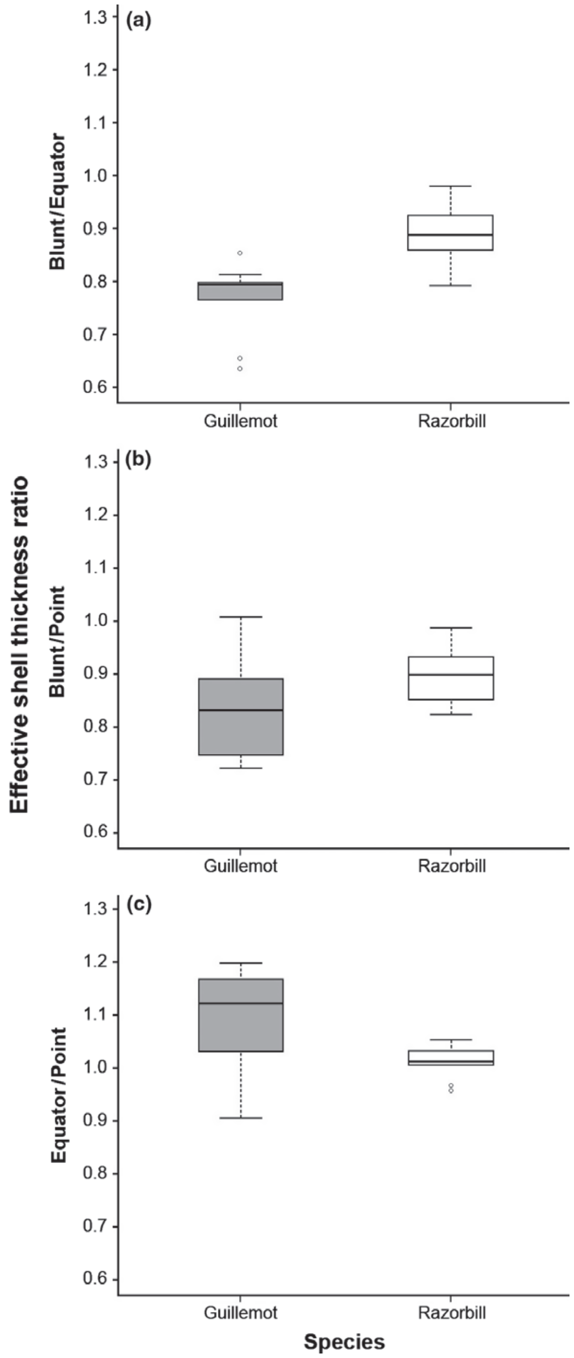


Figure 2. Effective shell thickness ratios between different regions of Guillemot and Razorbill eggs: (a) blunt/equator, (b) blunt/point, (c) equator/point. The Guillemot eggshell blunt/equator ratio (Welch's two-sample *t*-test; $t = 4.38$, df = 17, $P < 0.001$) and equator/point ratio (Welch's two-sample *t*-test; $t = 2.74$, df = 11, $P = 0.02$) are significantly different from that of Razorbill eggshells. There is no significant difference in blunt/point ratio between the two species (Welch's two-sample *t*-test; $t = 1.79$, df = 15, $P = 0.09$). A total of 20 ratios were analysed from 10 Guillemot and 10 Razorbill eggs.

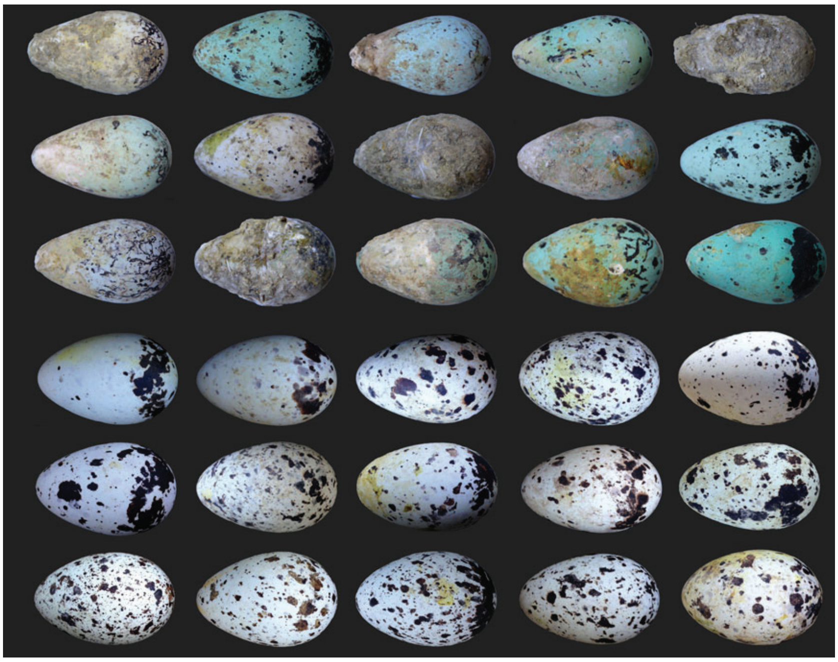


Figure 3. Examples of naturally incubated Guillemot (top three rows) and Razorbill (bottom three rows) eggs (n = 15 each), located haphazardly and photographed on the same ledge at approximately the same stage of incubation on Skomer Island, Wales (see text), to illustrate the extent of debris (both faecal and soil) contamination. The Guillemot eggs are more likely to be encrusted with faecal material and dirt, especially towards the pointed end of the egg. Some Razorbill eggs are contaminated with yellow material that we presume is a thin layer of faecal material, but not especially at the pointed end and none are encrusted in the same way as Guillemot eggs.

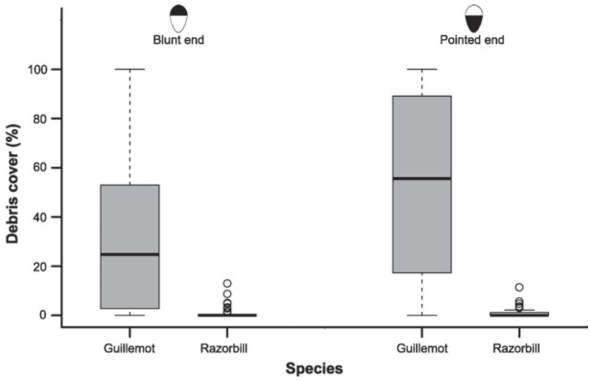


Figure 4. Extent of debris contamination on the eggs of Guillemots (n = 59) and Razorbills (n = 40) photographed part-way through incubation on Skomer Island, Wales (see Fig. 3). Contamination is significantly greater on Guillemot eggs, on both the blunt and the pointed ends, than on Razorbill eggs. Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values and open circles indicate potential outliers.

adaptation to reduce the risk of their falling off cliff ledges. We offer two new hypotheses to account for the pyriform shape of Guillemot eggs: that it provides resistance against impacts and protection from faecal and other contamination.

We obtained several results consistent with our first hypothesis that the Guillemot's pyriform egg shape confers strength and resistance against impacts. The pyriform shape of the Guillemot's egg results in a greater proportion of the egg surface area being in contact with the substrate than in the closely related Razorbill, which has less pear-shaped eggs. We propose that having a large proportion of the egg in contact with the substrate minimizes the 'stress concentration', that is, it disperses the consequences of any impact, which in turn reduces the likelihood of breakage resulting from an impact, particularly from above (Pilkey & Pilkey 2008). We suggest that the pyriform shape means that Guillemot eggs are relatively crush-proof in the region where impact is most likely.

As noted by several other authors, the eggshells of the Common Guillemot and Brünnich's Guillemot are, for their size, thicker than those of almost any other bird (Schoenwetter 1960–1992, Pirie-Hay & Bond 2014). We found Guillemot eggshells to be thickest at the equator and the pointed pole

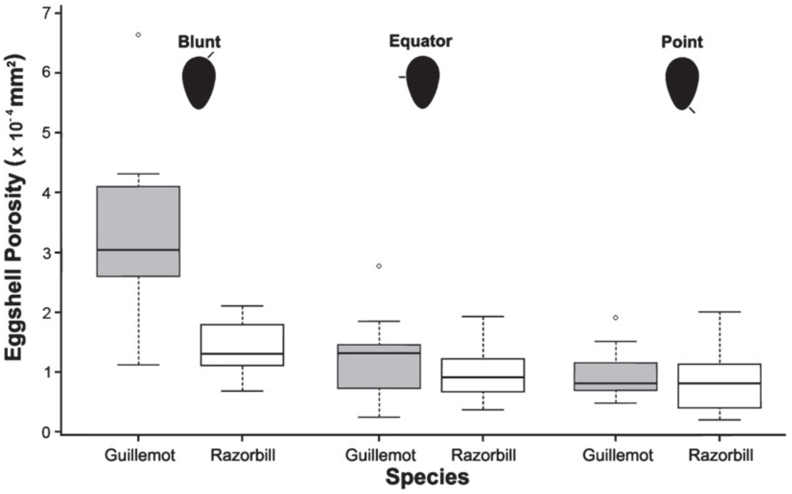


Figure 5. Porosity (total minimum pore area per mm^2) of Guillemot and Razorbill eggshells. The blunt end of Guillemot eggshells was significantly more porous than other egg regions ($P < 0.05$); Razorbill eggs were equally porous in all regions ($P > 0.05$). Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values and open circles indicate potential outliers. Ten Guillemot eggs and 10 Razorbill eggs were analysed and a mean value for each eggshell region (blunt, equator and point) was calculated, providing a total of 60 measurements.

(as did Maurer *et al.* 2012), essentially the area that lies in contact with the substrate during incubation. Indeed, as Maurer *et al.* (2012) found, although the blunt pole is thinner than the equator in the eggs of many of the 230 bird species they examined, that difference was most extreme in the Guillemot (also see Fig. 2). Our data show that the greater thickness at the equator is primarily due to an increase in effective shell thickness, rather than an increase in membrane or mammillary layer thickness (Fig. S3). This is also the case for the thickness at the pointed end, although an increase in membrane thickness contributes to the total thickness in this region. As greater shell thickness within a Guillemot egg is due to an increase in effective shell thickness, it is likely that the eggshell strength at the equator and pointed end is enhanced compared with the blunt pole. The blunt pole is less vulnerable to impact and, by being thinner, may enable the chick to emerge more easily from the shell. If it is true that a spherical egg has the greatest resistance to crushing (Smart 1969, Bain 1991), the enhanced shell strength at the equator and pointed end may be necessary to reinforce a potentially weak egg shape resulting from the Guillemot egg's elongation and deviation from a sphere (Maurer *et al.* 2012).

In reality, the minimization of the stress concentration by maximizing contact with the substrate, together with the increased shell thickness in the region of the eggshell where impact is most likely, must work together to create the Guillemot's robust eggshell, but it will require detailed experiments to establish the relative importance of these two features.

We also obtained evidence consistent with our second hypothesis that a pyriform shape provides some protection from debris contamination. In other species, debris contamination of eggshells can be fatal for the embryo, either because the pores in the eggshell become blocked and compromise gas exchange, or because of microbial infection (Verbeek 1984). The pyriform shape of the Guillemot's egg means that the blunt end of the egg is raised above the substrate surface and less likely to be covered in faecal material and/or soil than the pointed end. This may also explain the striking increase in porosity at the blunt end of the egg, which is also the end at which the chick's head is located in the later stages of incubation and from which the chick emerges from the shell (Tschanz 1968).

In a previous study, Zimmermann and Hipfner (2007) found no differences in pore density or pore size between the same three regions of Guillemot eggs as examined here. It seems likely that this discrepancy between their result and ours is a consequence of the methods used to assess porosity. For example, Zimmermann and Hipfner (2007) measured the area at the pore orifice on the inner surface of the shell, which we found to be on average 545 $\mu m^2 \pm 424$ greater than the minimum pore area measured using micro-CT. Although these two measures are weakly and positively correlated, the scatter is considerable (Fig. S4).

We have not, as yet, tested either hypothesis directly and two remaining questions are whether an elliptical-ovate egg (such as that of a Razorbill) of the same thickness as a Guillemot egg would confer the same degree of protection from impacts, and whether the elliptical-ovate Razorbill egg subjected to the same degree of faecal exposure as Guillemot eggs would suffer greater contamination of its blunt end and, as a result, reduced hatching success.

There are several reasons why the view that the pyriform shape of a Guillemot's egg is an adaptation to prevent rolling has been so pervasive. First, the idea is intuitively appealing, in part because single factor explanations are often preferred. Secondly, the rolling-in-an-arc idea gained traction initially because rolling was seen as a major mortality factor. However, this was a consequence of researchers such as Belopol'skii (1957) and Tuck (1961) using crude study methods (including walking on to the breeding ledges and firing guns at colonies), causing massive disturbance. Thirdly, the experimental results of Tschanz *et al.* (1969) helped perpetuate the rolling-in-an-arc idea, even after Tschanz's student and colleague, Ingold (1980), showed that those experiments were flawed. Finally, it is interesting that, in an overview, Tschanz (1990) agreed with Ingold that the Guillemot egg shape 'confers no greater advantage than a Razorbill egg on a Guillemot ledge (in preventing egg loss via rolling), but brooding behaviour does'.

Under normal circumstances, undisturbed guillemots of both *Uria* species very rarely leave their egg unattended and the risk of rolling is minimal, except during incubation changeovers, or sometimes during bouts of intraspecific aggression (e.g. Birkhead 1977, Gaston & Nettleship 1981, Harris & Wanless 1988). During incubation exchanges, Guillemots minimize the risk of egg-rolling by careful manipulation of the egg with their beak, retaining or sometimes transferring the egg between the tarsi, but also using their drooped wings to prevent the egg from rolling (Tschanz 1990, T.R. Birkhead pers. obs.). In addition, incubating Guillemots routinely accumulate small stones under and around the egg, which although dismissed as 'vestigial nest-building' (Tuck 1961) almost certainly provide additional stability to the egg. In many instances, because Guillemots breed in such close proximity, an egg that rolls away from an incubating bird will, when the colony is undisturbed, roll only as far as an immediate neighbour and be duly recovered. However, in the presence of predators such as Bald Eagles *Haliaeetus leucocephalus*, Red Foxes *Vulpes vulpes*, Arctic Foxes *Vulpes lagopus*, Polar Bears *Ursus maritimus* or humans, all of which can kill an adult Guillemot, it is hardly surprising that adult Guillemots (which are long-lived) look after their own safety and abandon their eggs (e.g. Birkhead & Nettleship 1995): under such circumstances no egg rolling adaptation can ensure the safety of an egg.

In summary, in light of the failure of the rolling-in-an-arc hypothesis to account for the pyriform shape of Guillemot eggs, we offer two new hypotheses: strength, and protection from debris contamination. We are not making a case for either one, and there may well be others (see Ingold 1980, Tschanz 1990). Indeed, it seems likely that the Guillemot's pyriform egg is a compromise between a number of different selection pressures.

We thank Chris Holland, Paul Ingold, Oleksandra Mykhaylyk, Tony Ryan and Craig Sturrock for helpful discussion; Skelet.AL lab for use of their micro-CT scanner; the Wildlife Trust of South and West Wales Trust for permission to work on Skomer Island NNR, Douglas Russell at the Natural History Museum, Tring, for access to eggs, and Nicola Hemmings, Bob Montgomerie and the referees for comments on the manuscript. This work was funded by a grant from the Leverhulme Trust to T.R.B.

REFERENCES

Andersson, M. 1978. Optimal egg shape in waders. *Ornis. Fenn.* **55**: 105–109.

Ar, A. & Rahn, H. 1985. Pores in avian eggshells: gas conductance, gas exchange and embryonic growth rate. *Respir. Physiol.* **61**: 1–20.

Bain, M.M. 1991. A reinterpretation of eggshell strength. In Solomon, S.E. (ed.) *Egg and Eggshell Quality*. Aylesbury: Wolfe Publishing Limited.

Bain, M.M. 2005. Recent advances in the assessment of eggshell quality and their future application. *Worlds Poult. Sci. J.* **61**: 268–277.

Belopol'skii, L.O. 1957. Ecology of Sea Colony Birds of the Barents Sea. Israel Program for Scientific Translations. Jerusalem. (Translated from Russian 1961).

Birkhead, T.R. 1977. The effect of habitat and density on breeding success in the Common Guillemot *Uria aalge*. *J. Anim. Ecol.* **46**: 751–764.

Birkhead, T.R. 1993. *Great Auk Islands*. London: Poyser.

Birkhead, T.R. 2016. *The Most Perfect Thing: the Inside (and Outside) of a Bird's Egg*. London: Bloomsbury.

Birkhead, T.R. & Nettleship, D.N. 1987. Ecological relationships between Common Murres, *Uria aalge* and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. II: breeding success and site characteristics. *Can. J. Zool.* **65**: 1630–1637.

Birkhead, T.R. & Nettleship, D.N. 1995. Arctic fox influence on a seabird community in Labrador: a natural experiment. *Wilson Bull.* **107**: 397–412.

Birkhead, T.R., Thompson, J.E. & Biggins, J.D. 2017. Egg shape in Common *Uria aalge* and Brünnich's Guillemots *U. lomvia*: not a rolling matter. *J. Ornithol.* DOI: 10.1007/s10336-017-1437-8

Board, R.G. 1982. Properties of avian egg shells and their adaptive value. *Biol. Rev. Camb. Philos. Soc.* **57**: 1–28.

Gaston, A.J. & Nettleship, D.N. 1981. *The Thick-billed Murres of Prince Leopold Island*. Ottawa: Canadian Wildlife Service Monographs, No. 6.

Gill, F. 2007. *Ornithology*. New York: Freeman.

Harris, M.P. & Birkhead, T.R. 1985. Breeding ecology of the Atlantic Alcidae. In Nettleship, D.N. & Birkhead, T.R. (eds) *The Atlantic Alcidae*: 155–205. London: Academic Press.

Harris, M.P. & Wanless, S. 1988. The breeding biology of guillemots *Uria aalge* on the Isle of May over a six year period. *Ibis* **130**: 172–192.

Hewitson, W.C. 1831. *British Oology: being Illustrations of the Eggs of British Birds*. Newcastle upon Tyne: Empson.

Ingold, P. 1980. Anpassungen der Eier und des Brutverhaltens von Trottelummen an das Brüten auf felssimen. *Z. Tierpsychol.* **53**: 341–388.

Kaftanovski, Y.M. 1941. Opyt sravnitel'noi kharakteristiki biologii razmnozhenyia nekotorykh chistikovykh. (Studies on comparative characteristics of the reproduction of some murre species). Trudy Gosudarstvennogo Zapovednika 'Sem'Ostrovov'. Glavnoe Upravlenie po Zapovednikam pri SNK RSFSR (Works by the 'Seven Islands' Sanctuary. Main Board of Reserves attached to Council of Comminssars for the RSFSR) **1**: 53072.

Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**: 116–121.

MacGillivray, W. 1852. *A History of British Birds*. London: Scott, Webster & Geary.

Maurer, G., Portugal, S.J. & Cassey, P. 2012. A comparison of indices and measured values of eggshell thickness of different shell regions using museum eggs of 230 European bird species. *Ibis* **154**: 714–724.

Nakagawa, S. & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Rev. Camb. Philos. Soc.* **85**: 935–956.

Pilkey, W.D. & Pilkey, D.F. 2008. *Peterson's Stress Concentration Factors*. New York: Wiley.

Pirie-Hay, D.W. & Bond, A.L. 2014. Thickness of Common Murre (*Uria aalge*) eggshells in Atlantic Canada. *Can. Field Nat.* **128**: 72–76.

Preston, F.W. 1953. The shapes of birds' eggs. *Auk* **70**: 160–182.

R Development Core Team. 2012. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org/

Riley, A., Sturrock, C.J., Mooney, S.J. & Luck, M.R. 2014. Quantification of eggshell microstructure using X-ray micro computed tomography. *Br. Poult. Sci.* **55**: 311–320.

Romanoff, A.J. & Romanoff, A.L. 1949. *The Avian Egg*. New York: Wiley.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**: 671–675.

Schoenwetter, M. 1960–1992. *Handbuch der Oologie*. Berlin: Akademie Verlag.

Smart, I.H.M. 1969. The method of transformed coordinates applied to deformations produced by the walls of a tubular viscus on a contained body: the avian egg as a model system. *J. Anat.* **104**: 507–518.

Smith, A. & Clarke, J.A. 2015. Systematics and evolution of the Pan-Alcidae (Aves, Charadriifornes). *J. Avian Biol.* **45**: 125–140.

Thomson, A.L. 1964. *A New Dictionary of Birds*. London: Nelson.

Todd, P.H. & Smart, I.H.M. 1984. The shape of birds' eggs. *J. Theor. Biol.* **106**: 239–243.

Tøien, Ø., Paganelli, C.V., Rahn, H. & Johnson, R.R. 1988. Diffusive resistance of avian eggshell pores. *Respir. Physiol.* **74**: 345–354.

Tschanz, B. 1968. *Trottellummen: Die Entstehung der persönlichen Beziehungen zwischen Jungvogel und Eltern*. Berlin: Paul Parey.

Tschanz, B. 1990. Adaptations for breeding in Atlantic Alcids. *Neth. J. Zool.* **40**: 688–710.

Tschanz, B., Ingold, P. & Lengacher, H. 1969. Eiform und Bruterfolg bei Trottellummen. *Ornithol. Beob.* **66**: 25–42.

Tuck, L.M. 1961. *The Murres: their distribution, populations and biology – a study of the genus Uria*. Ottawa: Canadian Wildlife Monograph Series, No. 1.

Uspenski, S.N. 1958. *The Bird Bazaars of Novaya Zemlya*. Ottawa: Department of Northern Affairs and Natural Resources, Canada (translated from Russian).

Verbeek, N.A.M. 1984. The effect of adult fecal material on egg hatchability in Glaucous-winged Gulls (*Larus glaucescens*). *Auk* **101**: 824–829.

Zimmermann, K. & Hipfner, J.M. 2007. Egg size, eggshell porosity, and incubation period in the marine bird family Alcidae. *Auk* **124**: 307–315.

Received 19 May 2016;
revision accepted 6 January 2017.
Associate Editor: Richard Phillips.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Method for calculating the 'contact index'.

Figure S1. Images illustrating how the contact index was calculated.

Table S1. Correlation coefficients between different measures of eggshell thickness.

Table S2. Repeatability values for eggshell thickness and porosity measures calculated according to the methods in Lessells and Boag (1987) and Nakagwa and Schielzeth (2010).

Figure S2. Cross sectional image of a piece of Guillemot eggshell showing the different shell thickness measures, taken using X-ray micro computed tomography.

Figure S3. Differences in effective shell thickness/total shell thickness ratios between the three regions of Guillemot and Razorbill eggs.

Figure S4. Relationship between minimum cross sectional pore area and inner pore orifice area.

CHAPTER 6:

Common guillemot (*Uria aalge*) eggs are not self-cleaning

Common guillemot (*Uria aalge*) eggs are not self-cleaning

Jackson, D., Thompson, J. E., Hemmings, N. and Birkhead, T. R. (2018). Common guillemot (*Uria aalge*) eggs are not self-cleaning. *Journal of Experimental Biology*, **221**, jeb188466.

Original article and Supplementary Materials can be found using the link below:

http://jeb.biologists.org/lookup/doi/10.1242/jeb.188466

Movies 1-3 referenced in this chapter can be viewed in the online published version of this manuscript at the above URL.

This chapter has been previously presented in a chapter for a PhD Thesis by Duncan Jackson entitled: '*The adaptive significance of avian eggshell architecture*'. The PhD thesis was submitted at The University of Sheffield in December 2019.

Chapter context and thesis author's contributions: A researcher had reported at a conference some unpublished observations that suggested that Common Guillemot eggshell surfaces has self-cleaning properties. This unpublished work was widely reported in the media stating that Common Guillemot eggs are indeed self-cleaning. Given that Common Guillemot eggs are often partially or totally covered in faecal material and other dirt on their breeding ledges (see **Chapter 5**), the self-cleaning idea seemed implausible. The overall aim of this study was therefore to test the self-cleaning properties of Common Guillemot eggshells. With regards to the proposed faecal/debris contamination adaptive hypothesis for the Common Guillemot's pyriform egg shape (presented in **Chapter 5)**, such adaptive selection would only occur if eggshell contamination by faecal/debris materials had a negative consequence on eggshell functions such as gaseous exchange. In part of this study, we test the effect of faecal/debris contamination on gas exchange across the Common Guillemot eggshell. We did this using a novel Fourier-transform infrared (FTIR) spectroscopy experimental set-up that measured carbon dioxide exchange rates across eggshell fragments. We make a clear case that Common Guillemot eggshells are not self-cleaning and show that faecal/contamination does reduce gas exchange, thus providing a possible selective pressure for the faecal/debris contamination adaptive hypothesis to function. However, to fully examine the plausibility of such a hypothesis would likely require certain egg manipulation experiments to establish whether faecal/debris contamination reduces hatching success, but we did not conduct such tests for ethical reasons.

In this study, I developed and performed the experiments using novel Fourier-transform infrared (FTIR) spectroscopy methods to examine how faecal/debris contamination affects the rates of carbon dioxide conductance across the Common Guillemot eggshell. I collated the data and performed preliminary statistical analyses on the FTIR experimental dataset before providing it to D. Jackson for finalised statistical analyses. I also commented and assisted with improving subsequent re-drafts of the manuscript.

Co-authors' contributions: T.R. Birkhead conceived the idea for this paper. D. Jackson researched and wrote the initial manuscript and improved subsequent re-drafts with assistance also from T.R. Birkhead and N. Hemmings. D. Jackson performed all microCT scanning and self-cleaning trials, in addition to experiments testing how shell accessory material prevents pore blockages. All the final statistical analyses and figures presented in the paper were performed by D. Jackson. N. Hemmings and T.R. Birkhead supervised the project.

© 2018. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2018) 221, jeb188466. doi:10.1242/jeb.188466

RESEARCH ARTICLE

Common guillemot (*Uria aalge*) eggs are not self-cleaning

Duncan Jackson*, Jamie E. Thompson, Nicola Hemmings and Timothy R. Birkhead

ABSTRACT

Birds are arguably the most evolutionarily successful extant vertebrate taxon, in part because of their ability to reproduce in virtually all terrestrial habitats. Common guillemots, *Uria aalge*, incubate their single egg in an unusual and harsh environment; on exposed cliff ledges, without a nest, and in close proximity to conspecifics. As a consequence, the surface of guillemot eggshells is frequently contaminated with faeces, dirt, water and other detritus, which may impede gas exchange or facilitate microbial infection of the developing embryo. Despite this, guillemot chicks survive incubation and hatch from eggs heavily covered with debris. To establish how guillemot eggs cope with external debris, we tested three hypotheses: (1) contamination by debris does not reduce gas exchange efficacy of the eggshell to a degree that may impede normal embryo development; (2) the guillemot eggshell surface is self-cleaning; (3) shell accessory material (SAM) prevents debris from blocking pores, allowing relatively unrestricted gas diffusion across the eggshell. We showed that natural debris reduces the conductance of gases across the guillemot eggshell by blocking gas exchange pores. Despite this problem, we found no evidence that guillemot eggshells are self-cleaning, but instead showed that the presence of SAM on the eggshell surface largely prevents pore blockages from occurring. Our results demonstrate that SAM is a crucial feature of the eggshell surface in a species with eggs that are frequently in contact with debris, acting to minimise pore blockages and thus ensure a sufficient rate of gas diffusion for embryo development.

KEY WORDS: Common murre, Faeces, Eggshell, Gas conductance, Incubation, Embryo development

INTRODUCTION

Birds breed in virtually all terrestrial habitats, from deserts to polar regions, and even in wet environments (Deeming, 2002). This flexibility in breeding ecology (specifically, in habitat use) can be attributed to the fact that birds lay hard-shelled, desiccation-resistant eggs in a nest (or other incubation site) that is generally attended by one or both parents (Deeming, 2002). A consequence of laying eggs into a nest, which is then attended by a parent, is that the microclimate eggs are incubated in, and the conditions the avian embryo experiences during development, are largely independent of the wider environment (Ar, 1991; Deeming and Mainwaring, 2016; Rahn et al., 1983; Rahn, 1991). In some species, however, bird eggs are exposed to extreme and potentially detrimental conditions due to the lack of a nest, limitations of incubation sites or parental behaviours (Board, 1982).

The common guillemot, *Uria aalge* (Pontoppidan 1763), breeds colonially on exposed and rocky cliff ledges which minimises predation of their eggs and chicks from terrestrial animals (Nettleship and Birkhead, 1985). To reduce the risk of losing eggs or chicks to aerial predators, guillemots also breed at very high densities (typically, 20 pairs m^{-2}) (Birkhead, 1977, 1993). One consequence of high density breeding is that colonies become ‘unhygienic’, with faecal material accumulating on the sea cliffs and breeding ledges. Contrary to previous suggestions (e.g. D’Alba et al., 2017), guillemot breeding sites are not usually dry, but are periodically wetted by rain, leading to the formation of dirty puddles on the breeding ledges (Fig. S1; T.R.B., personal observation). Since guillemots do not build a nest and instead incubate their single egg directly on bare rock ledges, their eggs are frequently exposed to a slurry of faeces, dirt, other detritus and water (henceforth ‘debris’) during incubation (Birkhead, 2016; Birkhead et al., 2017; Tschanz, 1990). Contamination of the eggshell by debris is almost inevitable as guillemots typically incubate their eggs between their legs (rarely with the egg entirely on top of their feet), and usually with the lower surface of the egg in direct contact with the substrate (Birkhead et al., 2018; Manuwal et al., 2001; Fig. S1).

Wet debris on the eggshell is likely to have a detrimental effect on embryonic survival since it may enter and block the gas exchange pores in the eggshell, reducing the gas exchange efficacy and also facilitate microbial invasion via the pore canals (Board, 1982). Both of these effects could compromise embryonic development through reduced water loss, CO_2 retention leading to hypercapnia (enhanced CO_2 in the embryo’s blood), asphyxiation or infection, and can ultimately result in embryo mortality (Ar and Deeming, 2009; Board and Fuller, 1993). Despite these potential risks, guillemot eggs covered with debris are known to hatch successfully (T.R.B., personal observations), suggesting that either the debris that guillemot eggs are exposed to is relatively benign and does not compromise embryo survival, and/or guillemot eggs possess adaptations to cope with the impact of debris.

Guillemot eggs could be unaffected by extensive debris cover if, due to intrinsic properties of the debris, it does not reduce the gas exchange efficacy of the shell. Coating either part of the blunt or pointed end of a chicken, *Gallus domesticus*, egg with a man-made impermeable material (epoxy cement) has been shown to increase embryo mortality and levels of hatching failure (Tazawa et al., 1971). However, natural debris that adheres to the eggshell comes from a variety of sources and may include faecal material (which varies in its composition depending on the bird’s diet, e.g. guillemot faeces contains small fish bones), dirt, sand, small stones, dust, feathers and vegetation. It is therefore likely to vary in gas permeability depending on its composition, and consequently may not have the same negative effects on embryo survival as impermeable cement.

Verbeek (1984) found that the water loss and hatching success of glaucous gull (*Larus glaucescens*) eggs were reduced when they were coated with gull faeces, but not when the eggs were coated with cormorant (*Phalacrocorax auritus* or *Phalacrocorax pelagicus*) faeces. This result is likely due to differences in the

Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK.

*Author for correspondence (djackson3@sheffield.ac.uk)

D.J., 0000-0003-4777-0275

Received 9 July 2018; Accepted 3 October 2018

composition of faeces between species, and therefore the ability of gases to diffuse through. As a result, Verbeek (1984) suggested that birds that direct their faeces away from the nest site during incubation (like glaucous gulls) produce faeces that would inhibit gas exchange if it covered their egg(s); defecating away from the incubation site may therefore have evolved in response to the negative impact of faeces on embryo development. Birds producing faeces that has little effect on eggshell conductance or hatching success may not be under the same selection to defecate away from their eggs or those of their neighbours in colonial breeding species. If Verbeek (1984) is correct, one might predict that guillemot faeces has little impact on gas exchange efficiency of the eggshell, since guillemots cannot not deliberately defecate away from their colony because they breed at such high densities. In fact, although they propel their faeces away from themselves, they regularly propel their faeces onto neighbouring birds and their eggs. In addition to faecal material, the debris on guillemot breeding ledges can include bones, stones, feathers, vegetation and soil, and thus may be porous and permeable to gases, allowing the relatively unrestricted diffusion of gases through it. However, if debris penetrates and blocks the gas exchange pores, it may still impede gas exchange by reducing the number of functional pores (open channels that allow the passage of gases through them) in the eggshell.

If guillemot eggs are affected by debris, one potential way they might cope is through 'self-cleaning' to remove contaminants, as suggested in observations by Steven Portugal and his team (https://phys.org/news/2013-07-unique-shell-guillemot-eggs-edge.html). Despite being widely covered by the media, including The Guardian (https://www.theguardian.com/science/small-world/2013/jul/18/nanotech-roundup-cosmetic-fix-micro-batteries), National Geographic (https://www.nationalgeographic.com/science/phenomena/2013/07/04/scientist-spills-water-discovers-self-cleaning-bird-egg/) and the BBC (article no longer available), this work remains unpublished (media reports were based on a conference presentation).

For a surface to be self-cleaning it must possess three properties: (1) high water repellency (known as super-hydrophobicity), with a stationary water contact angle of ∼150 deg; (2) low adhesion of extraneous debris to the eggshell surface; and hence (3) effortless removal of water and debris from the eggshell when water droplets make contact with its surface (Ensikat et al., 2011; Genzer and Marmur, 2008; Yuan and Lee, 2013). According to the unpublished findings, the surface structure of guillemot eggshells makes them super-hydrophobic and consequently, self-cleaning. If true, debris should simply leave the surface of the shell every time the guillemot eggshell makes contact with water. The idea that guillemot eggs are self-cleaning seems biologically implausible since most guillemot eggshells remain contaminated with debris during the incubation period (Birkhead, 2016; Birkhead et al., 2017), but the hypothesis has yet to be empirically tested.

If the guillemot eggshell is not self-cleaning, then the shell accessory material (SAM) on the surface of the eggshell could limit the impact of debris by preventing pore blockages (Board, 1982). Here, we use Board and Scott's (1980) more general terminology: 'shell accessory material' (henceforth, SAM), rather than 'cuticle' (implying organic material) or 'cover' (implying inorganic material), as SAM is semantically more appropriate (Board et al., 1977). SAM is the outermost substance that sits on the exterior surface of the eggshell and can provide a variety of benefits, including waterproofing (Board and Halls, 1973a,b; Sparks and Board, 1984), microbial defence (D'Alba et al., 2014; Gole et al., 2014a,b; Ishikawa et al., 2010; Wellman-Labadie et al., 2008), desiccation resistance (Deeming, 1987; Thompson and Goldie, 1990), aesthetic properties such as gloss (Igic et al., 2015), UV reflectance (Fecheyr-Lippens et al., 2015), colouration and patterning (Lang and Wells, 1987; Samiullah and Roberts, 2014) and, as a consequence, protection from harmful wavelengths of light (Lahti and Ardia, 2016; Maurer et al., 2015). SAM may also provide increased shell strength (Portugal et al., 2017; Tyler, 1969). This wide range of properties may be attributable to the composite nature of SAM, as well as its varied thickness and composition in different species (Mikhailov, 1997). Despite the variability that exists in SAM, D'Alba et al. (2017) showed that SAM may possess some universal functions including modulating UV reflectance and providing a barrier against microbes across seven bird species studied. However, it is not clear whether SAM can also provide a barrier to debris, specifically, whether or not SAM can prevent debris from entering pores and blocking them.

Board and Perrott (1982) provided circumstantial, observational evidence that SAM may prevent pore blockages by debris in naturally incubated guinea fowl (*Numidia meleagris*) eggs. However, no manipulations of eggshell structure were performed to explicitly test the hypothesis that SAM prevents pore blockages. The adaptive role of SAM in the common guillemot's egg is not clear (but see D'Alba et al., 2017 for suggestions). It is therefore unknown if SAM mitigates the negative costs of debris on the guillemot eggshell by, for example, preventing pores from becoming blocked.

The aim of the present study was to establish how common guillemot embryos survive incubation in eggs with large amounts of debris on their shell surface, by testing the following three hypotheses: (1) the properties of natural debris are such that contamination of the eggshell does not reduce the gas exchange efficacy of the shell; (2) the guillemot eggshell is self-cleaning; and (3) shell accessory material prevents pore blockages by debris, which in turn ensures sufficient gas exchange is permitted across the eggshell for embryonic development.

MATERIALS AND METHODS

Eggshell and debris sampling

Fresh eggs were collected in 2013–2016 under licence from Skomer Island, Wales, UK. All eggs were drained of their contents before being washed in distilled water and allowed to air dry at room temperature before storage. A hand-held rotary saw (Dremel Multi) was used to cut fragments (∼1 cm^2) from the eggshells for use in the experiments detailed below. Where possible, fragments were cut from areas of the eggshell that appeared to be clean and the fragments were then rinsed in distilled water and allowed to air dry. No soap or chemicals were used in the cleaning process as they can damage the surface of the shell and SAM (D.J., personal observation). Natural debris was opportunistically collected directly into sterile Eppendorf tubes from guillemot breeding ledges in 2014–2017. Debris was stored dry or semi-dry and rehydrated prior to use in experiments. All debris was used within one year of collection, typically sooner, within 1–2 months.

Effect of debris on eggshell gas conductance

Fragments from the blunt end (see Birkhead et al., 2017 for sampling location) of each egg were carefully fixed to individual custom glass vials with an aperture diameter of ∼0.3–0.5 cm using cyanoacrylate glue (Loctite, USA), so that the inside of the eggshell membrane was fixed to the glass vial, and left to dry for 24 h. The seal between the eggshell and the glass vial was checked before any excess shell around the edge of the glass vial was removed with a hand-held rotary saw. Finally, a further layer of glue was applied to the circumference of the eggshell fragment and glass vial and left to dry. Each fragment underwent two treatments, a 'clean' trial followed by a 'dirty' trial. Before clean trials, eggshell fragments were carefully cleaned on the outer surface using a fine paintbrush to remove any dust and debris. For dirty trials, rehydrated natural debris (1 g of natural debris mixed with 300 µl of distiller water) was applied to the outer eggshell surface of fragments using a paintbrush until they were evenly coated and no eggshell surface was visible.

A Bruker Alpha FTIR Spectrometer fitted with an Alpha-T module cell at a resolution of 0.8 cm^{-1} was used to record the spectra of gases within the glass vials. Sample scan and background scan times were set to 32 scans, the result spectrum was set to 'absorbance', and the resulting spectrum was saved from the 360–7000 cm^{-1} range. All spectra were baseline corrected using an independent background scan of laboratory air that was recorded before each series of measurements. To record the spectra readings, a glass vial with an eggshell fragment fixed to the top, was placed on to the extended finger of a gas cell (calcium fluoride windows, a 7 cm path length and one gas-tight 'Youngs' valve) and sealed using a petroleum-based jelly. To create the CO_2-rich environment inside the gas cell, small pieces of dry ice were initially placed into the cell before the attachment of the glass vial. To avoid a build-up of pressure while the dry ice sublimed, the gas-tight tap was opened slightly and the gas cell attached to a gas bubbler. Once the dry ice had completely sublimed and no further bubbles were observed inside the gas bubbler, the gas-tight tap was closed, and the gas bubbler removed. Immediately after this, the gas cell was positioned onto the Alpha-T cell sample holder on the Bruker Alpha FTIR and an absorbance spectrum was recorded and saved. Another spectrum was recorded and saved 1 h later to determine how much CO_2 had diffused through the shell within this time frame.

To quantify the rate constant of eggshell CO_2 gas diffusion for each fragment (henceforth, CO_2 conductance), integral measurements were taken within a range that is known to correspond to several CO_2 absorption bands (range set between 3482.5 and 3763.15 cm^{-1}) from the initial spectra and the spectra after 1 h for each individual sample (see https://webbook.nist.gov/chemistry/). Integral values were standardised so that the initial value was 100. The CO_2 conductance was calculated by subtracting the standardised integral after 1 h from the standardised initial integral.

The method described above was chosen over other methods to measure eggshell conductance of eggshell fragments (e.g. Portugal et al., 2010) for two main reasons. Firstly, it directly measures the amount of CO_2 gas lost through the eggshell rather than predicting gas loss from measured mass loss. This potentially provides more precise measurements as the precision of weighing scales can be more limiting than the FTIR spectrometer (J.E.T., personal observation), as well as providing more accurate data because gas loss is directly measured rather than predicted from mass loss. Secondly, and crucially, this method allowed us to repeat each trial on the same fragments when they were clean and dirty without damaging the fragment or the vessel the sample was attached onto, which would not be possible using Portugal et al.'s (2010) approach. Even though we are measuring the change in CO_2 loss, water vapour, oxygen and CO_2 conductance are all linked (Rahn and Paganelli, 1990; Ar and Deeming, 2009) so all gases are likely to be affected in a similar way and, therefore, any restrictions on CO_2 conductance can theoretically be more broadly applied to any gas crossing the shell.

After the gas conductance of dirty fragments was measured, we cut the eggshell fragment off the glass vial and used X-ray microcomputed tomography (microCT) to assess the extent to which eggshell pores were blocked by debris. Because the eggshell fragment needed to be cut off the glass vial for micro-CT scanning, we could not scan the eggshell fragments in between clean and dirty treatments, only once the gas conductance experiment was over and the eggshell fragment was dirty. Eggshell fragments were scanned in a Bruker Skyscan 1172 set to 100 kV electron acceleration energy and 90 µA current, with the sample 45.7 mm from the X-ray source with a 1.0 mm aluminium filter; and the camera 218 mm away from the source. Camera resolution was set at 1048×2000 pixels, and a pixel size of 4.87 µm. We used the same settings for each scan, collecting a total of 513 projection images over a 180 deg rotation using a rotation step size of 0.4 deg and a detector exposure of 885 ms integrated over three averaged images, resulting in a total scan time of 38 min. One eggshell fragment was scanned during each session. Projection images were reconstructed in NRecon software (version 1.6.10.2) after which image analysis was performed in CTAn (CT-analyser, version 1.14.41), CTVox (CT-Voxel, version 3.0) and CTVol (CT-Volume, version 2.2.3.0; all the above software was provided by Bruker micro-CT, Kontich, Belgium). Reconstruction parameters used were: dynamic image range; min. attenuation coefficient=0.0025, max.=0.05; level 2 asymmetrical boxcar smoothing; ring artefact correction=12; beam hardening correction of 20% and auto misalignment compensation. Resultant images were saved as 8-bit bitmaps.

Two 3D models – one for the shell and another for the debris – were created for each shell fragment by segmenting the images in CTAn. Shell models were created by initially resizing the dataset by a factor of 2, with averaging in 3D on, before using automatic (Otsu's method) thresholding to segment the images, followed by low level despeckling of white and black pixels in 2D space (<10 pixels). The 3D model was then created using an adaptive rendering algorithm with smoothing on, a locality value of 1 and a tolerance of 0.05, and then saved as a .ctm file. Debris models were created by initially resizing the dataset by a factor of 2, with averaging in 3D off, before manually thresholding for debris to segment the images, followed by low level despeckling of white (<2 pixels) and black (<10 pixels) pixels in 2D space (<10 pixels). Again, the 3D model was then created using an adaptive rendering algorithm with smoothing on, a locality value of 1 and a tolerance of 0.05, and saved as a .ctm file. Both models were loaded into CTVol, aligned and pore channels were visually inspected to see if they were blocked by debris (Fig. S2). Owing to the image processing protocols followed, we could detect air spaces (and blockages) no smaller than 10 µm, so our method may have overestimated the number of blocked pores since any pores with small air spaces within the debris blockage would have been undetectable at the resolution limit. This measure is therefore a proxy of the level of pore blockages within an eggshell fragment, rather than an absolute value. This methodology may introduce a bias if different types of debris are studied, but in each of our experiments debris was used from a single sample collected from the field, removing this issue. Only blockages inside the pore channel were counted, and not blockages at the surface of the pores, because the thresholding parameters used to identify debris could not distinguish between debris and the shell membranes, and potentially SAM on the shell surface.

The number of blocked pores was divided by the total number of pores to provide an estimate of the proportion of blocked pores per fragment. The thickness of debris on the surface of the shell (above each pore), and the length of each pore channel was measured in CTAn using the line measurement tool and averaged for each eggshell fragment. The thickness of the true shell (the calcium carbonate layers of the eggshell, excluding the organic membranes) was also measured at 10 locations using the line measurement tool and averaged for each fragment (see Birkhead et al., 2017).

Self-cleaning eggs

Using a method similar to Vorobyev and Guo (2015), we tested the most important property of self-cleaning surfaces: whether water droplets and debris readily leave the guillemot eggshell surface together. Ten freshly collected guillemot eggshells and five museum samples were used in this study. Fragments were taken from the equator of each eggshell (see Birkhead et al., 2017), and two fragments per eggshell were studied per treatment. An eggshell fragment was attached to a stand tilted at 8 deg and dust from a household vacuum cleaner (as used in Vorobyev and Guo, 2015), was applied to the shell's surface. In a series of 15–20 droplets, 400 µl of water was dripped on to the fragment and the shell was examined by eye. If the eggshell fragment contained a puddle of water carrying floating or stationary dust then the surface was deemed to not be self-cleaning, as water and debris still remained on the surface (see Introduction for definition of self-cleaning). If the surface did not contain any floating dust particles or any water, then the surface was classified as self-cleaning (Vorobyev and Guo, 2015). To validate this simple self-cleaning test, we repeated this trial using the following known self-cleaning materials; the fresh, young leaves of cauliflower (*Brassica oleracea var. botrytis*), broccoli (*Brassica oleracea var. italica*) and collard (spring) greens (*Brassica oleracea var. viridis*). After the dust trial on *Brassica* leaves, very little or no water remained on the surface of the leaves as it bounced off the samples removing debris with it (Movie 1), therefore validating the use of this simple self-cleaning test to determine if guillemot eggshells are self-cleaning. Self-cleaning tests were repeated using wet debris (a vial containing 2.5 ml of semi-dry natural debris was diluted with 100 µl of distilled water) and debris that had been allowed to dry onto the shell to assess if guillemot eggshell is self-cleaning against natural debris it would encounter during incubation.

After the self-cleaning experiment was conducted, eggshell fragments were washed in excess water and allowed to dry, to mimic a heavy rain shower and followed by natural drying. Eggshell fragments were then qualitatively assessed (yes, or no) – by eye, using a macro lens on a digital camera, and by microscope – to establish whether any debris remained on the shell surface.

Shell accessory material and pore blockages

To test the role of shell accessory material in preventing pore blockages by debris, we chemically manipulated eggshell fragments to remove shell accessory materials from the eggshell. Two pieces of shell (~1 cm^2) were cut from the equator of five fresh eggs (see Birkhead et al., 2017 for sampling location). One fragment acted as a control, and was washed in distilled water only, whereas the other fragment was first treated with thick household bleach (containing sodium hydroxide and hypochlorite) to remove organic shell accessory material (see Fig. S3), and then also washed in distilled water. Both the sodium hydroxide and sodium hypochlorite components of bleach have been used to remove organic shell accessory material from the surface of the shell in previous studies (Deeming, 1987; Tullett et al., 1976). Following the cleaning treatments, debris was carefully added to the surface of each shell fragment by squeezing a paintbrush loaded with wet debris (1 g of natural debris mixed with 300 µl of water) with forceps. The debris was allowed to air dry for at least 24 h.

Eggshell fragments were scanned in a Bruker Skyscan 1172 using similar settings as detailed above, except that in this case a pixel size of 4 µm was used; thus the sample was 48.7 mm from the X-ray source with a 1.0 mm aluminium filter, and the camera was 283 mm away from the source. We collected 499 projection images each with an exposure time of 1475 ms, leading to a scan time of 49 min. These settings provided higher resolution data compared with those used above. A lower pixel size had to be used to scan the fragments used in the gas conductance trials to ensure that all of the eggshell exposed over the hole in the glass vial was scanned, whereas this was not a limitation here.

Two 3D models were created per shell fragment (one for the shell and another for the debris) in CTAn by thresholding for each material (automatically for the shell using Otsu's method and manually for debris). Model creation parameters were the same as those discussed earlier except that shell models were created by initially resizing the dataset by a factor of 2 with averaging in 3D off. To account for differences in pore numbers between pairs of fragments, only the first 15 pores that could be visualised by re-slicing the *z*-stack of reconstructed images were selected to assess pore blockages. The models were then loaded into CTVol, and pore channels were visually inspected to see if they were blocked by debris model (Fig. S2). As explained above, this measure provides a proxy rather than the absolute number of blocked pores. However, since we were able to use a higher scanning (and model) resolution in this experiment, detection of pore blockages and air spaces in between debris should have a limit of ~8 µm.

Statistical analysis

All statistical analyses were performed in R (version 3.3.1, http://www.R-project.org). We used a paired *t*-test to test whether the presence of debris on the eggshell influenced CO_2 conductance. We used Pearson's product moment correlations to establish whether a correlation existed between the clean eggshell CO_2 conductance and the number of pores in an eggshell fragment or the length of those pores (measured both directly and by using the proxy of shell thickness). Pearson's product moment correlations were also used to establish whether a correlation existed between the relative change in CO_2 loss between clean and dirty fragments and the proportion of pores blocked in an eggshell fragment, or the thickness of the debris on the surface of the shell. Finally, paired *t*-tests were performed to assess whether SAM on the surface of guillemot eggshells limits the number of pores that are blocked by wet debris when it is applied to the outer surface of the shell.

RESULTS

Effect of debris on eggshell gas conductance

The rate of gas exchange for clean eggshell fragments was positively correlated with the number of pores present in an eggshell fragment (r=0.733, P=0.016, n=10), but not with either the mean length of pores (r=0.045, P=0.902, n=10), nor the mean trueshell thickness (r=−0.185, P=0.610, n=10). After debris was applied to the eggshell, CO_2 conductance significantly decreased (t=3.02, d.f.=9, P=0.014; Fig. 1). The relative reduction in CO_2 conductance of the eggshell after the application of debris was negatively correlated with the proportion of pores in the eggshell that were blocked (r=−0.821, P=0.004, n=10), with fragments possessing a greater proportion of blocked pores showing a greater reduction in CO_2 conductance compared with when the fragments were clean (Fig. 2). The reduction in CO_2 conductance was not related to the average thickness of the debris on the eggshell above each pore (absolute difference in CO_2 conductance: r=−0.160, P=0.66, n=10; relative difference: r=−0.21, P=0.56, n=10).

Self-cleaning eggs

None of the common guillemot eggshell fragments studied here demonstrated any self-cleaning ability against dust. All fragments were covered in a puddle of water containing dust at the end of the

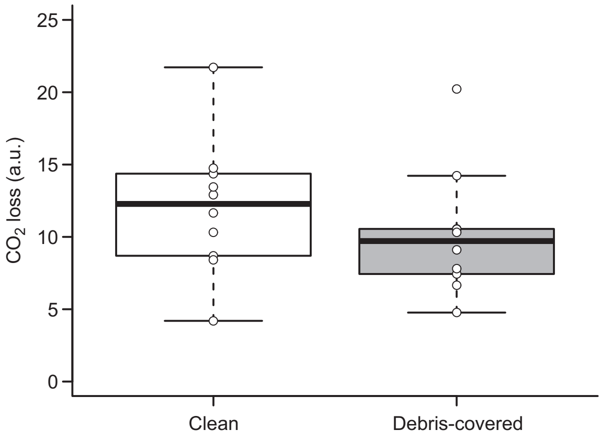


Fig. 1. The effect of debris on CO_2 loss through common guillemot eggshell. The rate of CO_2 loss significantly decreased after the application of natural debris onto the eggshell (paired *t*-test: $t=3.02$, d.f.=9, $P=0.0144$, $n=10$). Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values and the circles are the individual data points. a.u., arbitrary units.

trial, which is characteristic of materials that are not super-hydrophobic and not self-cleaning (Movie 2; Vorobyev and Guo, 2015). None of the guillemot eggshell fragments demonstrated any self-cleaning ability against either wet or dry natural debris (Fig. 3; Movie 3). It was possible to remove some debris – but not all – by washing the eggshell with water, but a large volume of water had to be applied and debris removal appeared to depend on water volume and/or pressure. This is not necessarily biologically relevant with respect to the circumstances in which guillemots breed because even when it is raining, it is unlikely that a large volume of pressurised clean water will make contact with the eggshell surface all at once. Instead, it is more likely that dirty water and wet debris from the cliff ledges will come into contact with the egg. Even after excessive washing, fragments were not completely clean, with small amounts of debris and staining remaining (Figs 3,4).

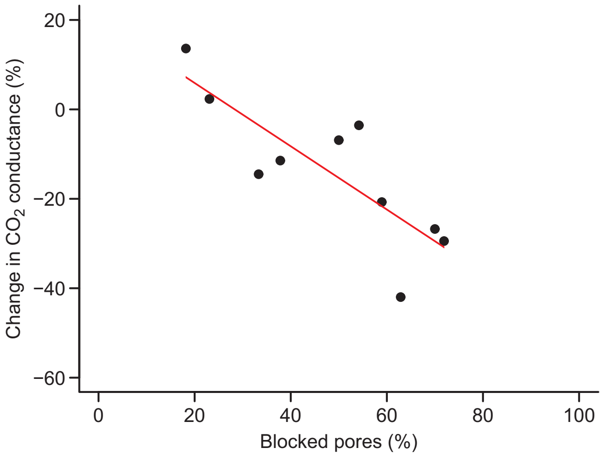


Fig. 2. The effect of blocked pores on CO_2 conductance through guillemot eggshell. The relative reduction in CO_2 conductance of the eggshell after the application of debris is negatively correlated with the proportion of pores in the eggshell that are blocked (Pearson's product moment correlation: $r=-0.821$, $P=0.004$, $n=10$). Change in CO_2 conductance was calculated as: [('dirty' gas conductance−'clean' gas conductance)/'clean' gas conductance]×100. The red line is the line of best fit.

Shell accessory material and pore blockages

The removal of SAM from eggshell fragments resulted in a significant increase in the proportion of pores that were blocked after the experimental application of natural debris to the shell surface, compared with control fragments where SAM was still present ($t=4.74$, d.f.=4, $P=0.009$; Fig. 5).

DISCUSSION

Our results show that debris contaminating the surface of guillemot eggshells during incubation reduces the gas exchange efficacy of the eggshell, and the eggshell is not self-cleaning to help resolve this problem. Instead, the full impact of debris on the gas exchange efficacy of eggshell is minimised by shell accessory material (SAM). SAM protects pores, reducing the number that are blocked by debris, which in turn minimises the reduction in eggshell gas conductance caused by debris on the eggshell.

The drivers of eggshell gas conductance

Our data suggest that pore number is the primary driver of gas conductance in guillemot eggshell fragments. This is contrary to the predictions of Zimmerman and Hipfner (2007) who suggest that shell thickness (i.e. pore length) and pore size are the key drivers of porosity and therefore gas conductance in common guillemot eggs. The fact that pore length (shell thickness) does not drive eggshell gas conductance is consistent with ideas initially presented by Ar and Rahn (1985) and Rahn and Paganelli (1990), as well as in the discussions of Portugal et al. (2010) and Maurer et al. (2012), which allude to the fact that shell thickness is not a determinant of water vapour conductance. In the present study, we were unable to use micro-CT to scan clean fragments that were used in our gas conductance trials (see Materials and Methods for further details), so we cannot explicitly link pore size to eggshell conductance. However, evidence from other studies suggests that the role of pore size is likely to be minor compared with that of pore number or density (Ar and Rahn, 1985; Rahn and Paganelli, 1990; Rokitka and Rahn, 1987; Simkiss, 1986; see Table 1).

If pore number is the main driver of gas conductance across the eggshell, then predictions made using the calculations based on the traditional theoretical formulae presented in Ar et al. (1974) and Ar and Rahn (1985), based on Fick's law of diffusion, may be incorrect as they erroneously include terms for pore length (shell thickness) and pore area. Previous research has suggested that calculated versus measured conductance values are not consistent; in fact, measured values can be three times lower than calculated values (Tøien et al., 1988). Inclusion of pore size and pore length (shell thickness) could be one reason for this discrepancy, alongside a lack of consideration of the effects of (1) SAM (Thompson and Goldie, 1990; Tøien et al., 1988), (2) convective and diffusive resistance (Tøien et al., 1988), and (3) internal heat changes due to the metabolic rate of the developing embryo. In addition, historical methods used to study shell thickness and porosity were imprecise, unreliable and inaccurate. For example, pore size was likely overestimated in previous studies because the minimum cross-sectional dimensions (e.g. area or radius) could not always be measured as they are within the pore channel, and therefore measures from the inner surface of the shell were used instead under the presumption that these dimensions were the limiting dimensions (see Birkhead et al., 2017). Furthermore, shell thickness measures are not always the same as pore length (see datasets 1 and 2).

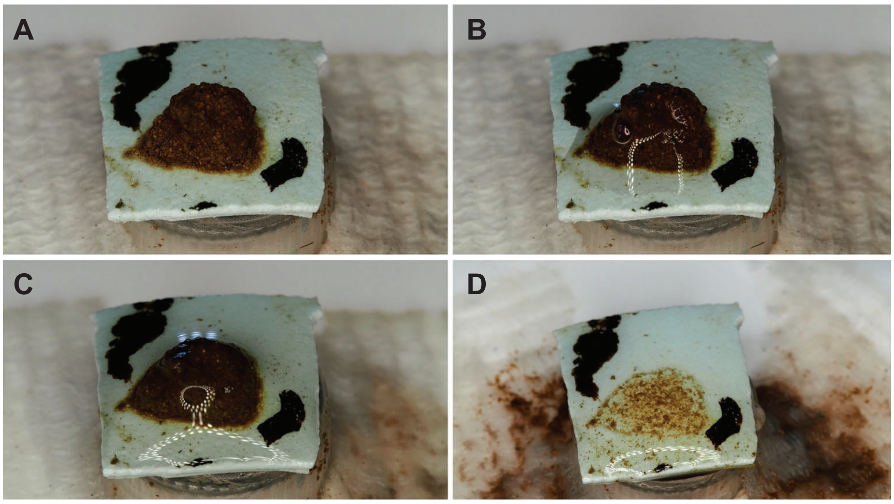


Fig. 3. A self-cleaning trial involving debris dried on to guillemot eggshells. (A) An eggshell fragment with debris on the surface. (B) The same fragment after the first drop of water has fallen onto the shell surface. (C) At the end of the trial, water and debris remain on the eggshell surface, illustrating that the sample is not self-cleaning. (D) After the trial, excess clean water was used to wash off the debris. Even after this cleaning, debris remains on the eggshell surface as stains or remnants. The large patch in the centre of the eggshell fragment is the debris; the two smaller dark patches either side are pigment on the eggshell surface. Eggshell sample is ~1 cm^2.

Further investigation into the drivers of eggshell gas conductance is needed, particularly with the advent of more precise and accurate methods for measuring eggshell parameters and gas conductance. Gaining a better understanding of what drives eggshell conductance is particularly important because predicted gas conductance values are used in a variety of ways, including for inferring the nesting conditions of extinct birds and dinosaurs (e.g. Deeming, 2006; Deeming and Reynolds, 2016) and drawing comparative conclusions about species' developmental biology (e.g. Jaeckle et al., 2012).

The role of shell accessory materials in protecting pores

Our finding that eggshell gas conductance is driven by pore number is important because it means that any blockages within pores impose a serious restriction on gas exchange by reducing the number of functional pores (i.e. unblocked, complete pores that gases can diffuse through) available for gas exchange. Our results show that blockage of pores by debris has a direct effect on the gas exchange efficacy of the eggshell, as was previously suggested by Board (1982) and Board and Perrott (1982). In a previous study, we suggested that the pyriform shape of common guillemot eggs, and the distribution of pores across the eggshell, may help to minimise the effects of eggshell contamination on the developing embryo (Birkhead et al., 2017). The orientation of the guillemot's pyriform egg during incubation is such that the blunt end of the egg (where porosity is highest) generally does not come into contact with the substrate, so most debris is concentrated on the pointed end of the egg where porosity is low. This potentially minimises the overall number of pores that become blocked and maximises the number of functional pores available for gas

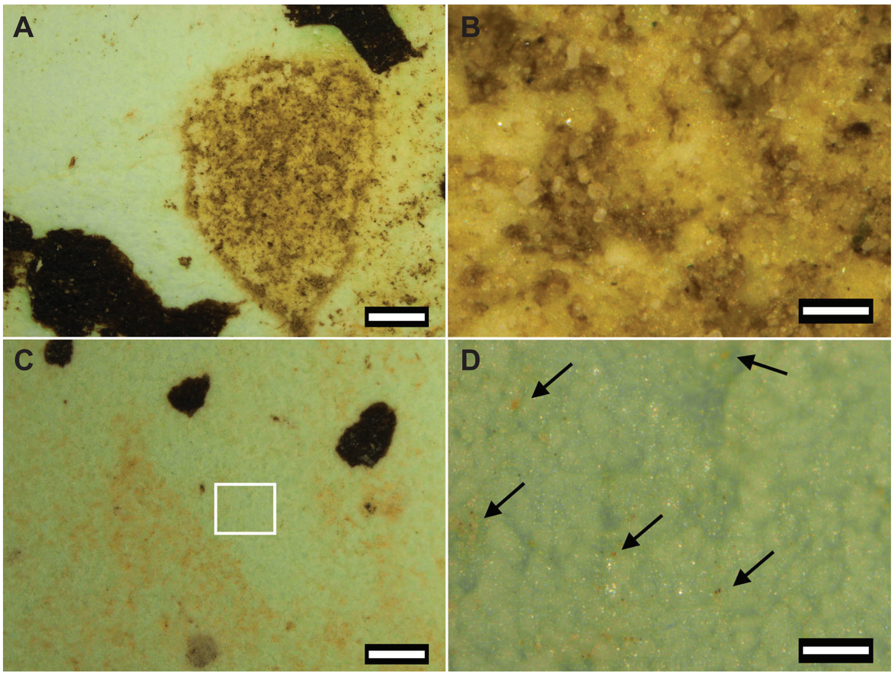


Fig. 4. Natural debris on common guillemot shells. (A,B) Stereoscopic microscopy images showing the remnants of debris remaining on a guillemot fragment after washing with excess water. (C,D) Stereoscopic microscopy images showing natural debris on common guillemot eggshell. The unmanipulated piece of guillemot eggshell in C shows natural debris staining, but also a patch that, to the naked eye, looks clean. The rectangle marks the 'clean' area shown in the high magnification image (D). There are in fact small particles of debris on the shell surface, a few of which are marked with arrows. Debris is light brown; darker brown/black patches in all images are eggshell pigment. Scale bars: 1000 μm (A,C) and 100 μm (B,D).

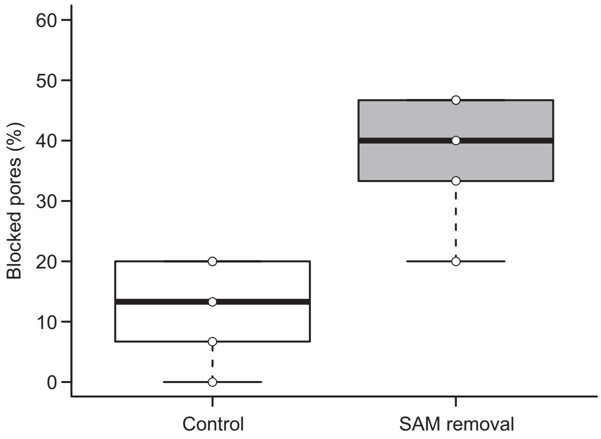


Fig. 5. Removal of shell accessory material increases the number of pores blocked by natural debris. The proportion of pores blocked by debris significantly increased after the removal of shell accessory material using bleach (paired *t*-test: *t*=4.74, d.f.=4, *P*=0.00904, *n*=5). Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values, and the circles are the individual data points.

exchange. However, debris on the elongated, pointed end of the egg could still lead to a large reduction in overall eggshell gas exchange, and, despite the egg's shape, debris is still sometimes seen on the blunt end. We show here that SAM prevents pores becoming blocked by debris, a finding consistent with Board and Perrott's (1982) observations that nesting debris penetrates pores and may reduce the total area of eggshell available for gases to diffuse through. SAM could therefore minimise the negative effects of debris covering the eggshell surface by minimising the number of pores that become blocked.

How SAM prevents pore blockages is not clear. One possibility is that the SAM acts as a physical barrier to the penetration of debris, as seemed to be the case for helmeted guinea fowl eggs (Board and Perrott, 1982). Alternatively, SAM may provide water resistance to the eggshell, which prevents aqueous debris from entering eggshell pores (Board, 1981). Either way, if SAM is removed or damaged, the pores become vulnerable to blockages. Natural cracking of SAM can occur due to dehydration, and cracks could leave pores vulnerable, which may explain why some of the untreated eggshell fragments we studied to assess the impact of debris on eggshell conductance had a large proportion of blocked pores (see Fig. S4). Some eggshells also had poor quality SAM or a patchy SAM coverage meaning pores were uncovered and left vulnerable (Fig. S3), and in addition, our limited imaging and blockage detection resolution may have led us to consistently overestimate the proportion of blocked pores (see Materials and Methods). Although this would not invalidate our overall findings, it could explain the unexpectedly high proportion of blocked pores found in untreated eggshells when debris was added onto the surface of the shell. Whether SAM plays the same role on the eggs of other species that are directly exposed to debris (e.g. the blue footed booby, *Sula nebouxii*; Mayani-Parás et al., 2015), remains to be tested.

Guillemot eggs are not self-cleaning

Despite suggestions of previous researchers, we found no evidence that the guillemot eggshell surface is self-cleaning. Common guillemot eggshells lack the three important properties which would make them self-cleaning. (1) They are not super-hydrophobic. Reported water contact angles are lower than 150 deg. For example, Portugal and colleagues reported values of approximately 120 deg (see http://phenomena.nationalgeographic.com/2013/07/04/scientist-spills-water-discovers-selfcleaning-bird-egg/) while D'Alba et al. (2017) reported values of just over 90 deg. The latter is potentially lower due to eggshell treatment with 70% alcohol in that study. (2) Debris strongly adheres to the guillemot eggshell surface (see fig. 3 in Birkhead et al., 2017). Our self-cleaning trials corroborate observations that debris cannot easily be washed off most guillemot eggshells. Instead, scrubbing or wiping with excess amounts of clean water is required to remove debris, and this is still often unsuccessful, implying that debris has high adhesion with the shell (J.E.T. and D.J., personal observations). Furthermore, it is worth noting that even

Table 1. Linear regression relationships between measured or calculated eggshell parameters and observed gas conductance in the eggs of 21 Anatidae species

Parameter	Calculation	Adjusted R^2	Regression equation	*P*-value	Source
Total pore circumference* (µm)	2π×pore radius×pores per egg	0.633	*y*=0.0153*x*+5.35	<0.0001	Recalculated from Hoyt et al. (1979) using formula from Simkiss (1986)
Calculated gas conductance‡ (mg day^{-1} Torr^{-1})	(2.24×pore area×pores per egg)/shell thickness	0.371	*y*=0.575*x*+9.41	0.00202	Calculated by Hoyt et al. (1979)
Total pore area (µm^2)	Measured pore area×pores per egg	0.485	*y*=0.0079*x*+9.63	0.000271	Calculated from data in Hoyt et al. (1979)
Pores per egg§	Calculated from surface area and measured pore density	0.624	*y*=0.00157*x*+2.52	<0.0001	Data from Hoyt et al. (1979)
Shell thickness (mm)	Measured directly from shell	0.267	*y*=56.7*x*−3.32	0.00968	Data from Hoyt et al. (1979)
Pore area (µm^2)	Average measured area of a pore	0.00479	*y*=0.0143*x*+14.5	0.308	Data from Hoyt et al. (1979)

The total number of pores per egg (R^2=0.624) and the total pore circumference (R^2=0.633) explain more variation in observed gas conductance than does calculated gas conductance using the traditional calculation (R^2=0.371), highlighting an issue with the assumption that pore area and shell thickness are determinants of gas conductance. The fact that total pore area per egg (R^2=0.485) explains less variation than the total number of pores per egg, and pore area is not significantly associated with observed gas conductance, suggests that pore area does not drive eggshell gas conductance.

*Based on Stefan's law of diffusion.

‡Constant×total pore area×pore length^{-1} based on Fick's law of diffusion.

§It is worth noting that Ar and Rahn (1985)'s regression analysis of pore number against eggshell gas conductance on eggs from 134 different species had an R^2 value of 0.89.

apparently clean sections of naturally incubated eggs usually contain staining or particles of debris when viewed at high magnification, illustrating that debris does indeed adhere to the eggshell surface (Fig. 4). (3) Consequently, natural debris on the guillemot eggshell surface does not readily leave when water makes contact with it and the eggshell (Fig. 3; Movie 3).

The fact that guillemot eggshells do not possess self-cleaning properties becomes intuitive when we consider how debris interacts with the eggshell surface. A single application of wet debris can not only cover the eggshell surface, but can also cause pore blockages that reduce the ability of gases to pass through the shell. A self-cleaning surface on its own would thus be insufficient to maintain adequate gas exchange across the eggshell, unless there was also a unique mechanism to unblock pore channels. Given that SAM prevents pore blockages, and that the presence of debris does not appear to limit the ability of gases to diffuse across the eggshell, there would be little selection on guillemot eggshell structure for self-cleaning properties in the context of eggshell conductance.

Instead of evolving self-cleaning eggs, guillemots may avoid the problem of their eggs becoming excessively covered in debris during incubation via an altogether different mechanism: egg turning. Egg turning is the process where incubating parents turn their eggs around along the longitudinal axis, which is important for normal embryonic development and subsequent hatching (Deeming and Reynolds, 2016). Turning may physically remove debris via abrasion and limit an excessive build-up of material on the surface of the shell (Board and Scott, 1980; Board, 1982; Board et al., 1984), which could affect embryo development by reducing gas conductance, increasing the risk of embryonic infection or interfering with contact incubation and thermoregulation. Anecdotal observations suggest that incubation and egg turning limits the build-up of material on common guillemot eggs, as abandoned, un-incubated eggs soon become completely covered in debris (T.R.B., personal observations; see Fig. S1 for an example). Furthermore, Verbeek (1984) suggested that abrasion of faecal material from the surface of glaucous gull eggs may have partially restored their hatching success, although this was not based on direct experimental evidence. However, guillemot eggs that are partially or largely covered with debris still tend to hatch (T.R.B., personal observation), indicating that complete debris removal is not essential for normal embryo development in this species.

Conclusion

The findings of the present study suggest that the effect of debris contaminating the surface of common guillemot eggs is minimised by the presence of SAM, which reduces the number of pores that become blocked. This, in combination with the fact that the pyriform shape of the guillemot egg minimises the amount of debris that covers the highly porous blunt end of the egg (Birkhead et al., 2017), ensures that a high proportion of pores remain functional during incubation and guillemot eggs are able to maintain efficient gas exchange despite being covered in debris. The ability of SAM to minimise pore blockages by debris, rather than the egg's shape or pore distribution, is presumably crucial when eggs are heavily covered with debris. It seems likely that the presence of functional SAM, rather than solely the egg's shape, allows guillemot eggs to maintain gas exchange despite being covered in debris throughout the 32 day incubation period, allowing the embryo to develop normally.

Acknowledgements
We thank the Skelet.AL lab for use of their micro-CT scanner; Thomas W. Smith and Dr Michael Hippler in the Department of Chemistry at the University of Sheffield for their guidance and assistance in conducting the gas conductance experiments using FTIR, the Wildlife Trust of South and West Wales Trust for permission to work on Skomer Island NNR, and Natural Resources Wales (NRW) for licences to take eggs for scientific purposes. We also thank Professor Ben Hatchwell and the referees for comments on the manuscript.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: T.R.B.; Methodology: D.J., J.E.T., N.H., T.R.B.; Formal analysis: D.J., J.E.T.; Investigation: D.J., J.E.T.; Resources: T.R.B.; Data curation: D.J.; Writing - original draft: D.J.; Writing - review & editing: J.E.T., N.H., T.R.B.; Visualization: D.J.; Supervision: N.H., T.R.B.; Project administration: D.J.; Funding acquisition: D.J., T.R.B.

Funding
This work was funded by a grant from the Leverhulme Trust to T.R.B. and a University of Sheffield Postgraduate Scholarship to D.J. N.H. was supported by a Patrick & Irwin-Packington Fellowship from the University of Sheffield and a Royal Society Dorothy Hodgkin Fellowship.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.188466.supplemental

References
Ar, A. (1991). Roles of water in avian eggs. In *Egg Incubation: Its Effect on Embryonic Development in Birds and Reptiles* (ed. D. C. Deeming and M. W. J. Ferguson), pp. 229-244. Cambridge: Cambridge University Press.

Ar, A. and Deeming, C. D. (2009). Roles of water and gas exchange in determining hatchability success. *Avian Biol. Res.* **2**, 61-66.

Ar, A. and Rahn, H. (1985). Pores in avian eggshells: gas conductance, gas exchange and embryonic growth rate. *Respir. Physiol.* **61**, 1-20.

Ar, A., Paganelli, C. V., Reeves, R. B., Greene, D. G. and Rahn, H. (1974). The avian egg: water vapor conductance, shell thickness, and functional pore area. *Condor* **76**, 153-158.

Birkhead, T. R. (1977). The effect of habitat and density on breeding success in the common guillemot, *Uria aalge*. *J. Anim. Ecol.* **46**, 751-764.

Birkhead, T. R. (1993). *Great Auk Islands*. London, UK: Poyser.

Birkhead, T. R. (2016). *The Most Perfect Thing: The Inside (and Outside) of a Bird's Egg*. London, UK: Bloomsbury.

Birkhead, T. R., Thompson, J. E., Jackson, D. and Biggins, J. D. (2017). The point of a Guillemot's egg. *Ibis* **159**, 255-265.

Birkhead, T. R., Thompson, J. E. and Montgomerie, R. (2018). The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *Auk* **135**, 1020-1032.

Board, R. G. (1981). The microstructure of avian eggshells, adaptive significance and practical implications in aviculture. *Wildfowl* **32**, 132-136.

Board, R. G. (1982). Properties of avian egg shells and their adaptive value. *Biol. Rev.* **57**, 1-28.

Board, R. G. and Fuller, R. (1993). *Microbiology of the Avian Egg*. London, UK: Chapman and Hall.

Board, R. G. and Halls, N. A. (1973a). The cuticle: a barrier to liquid and particle penetration of the shell of the Hen's egg. *Br. Poult. Sci.* **14**, 69-97.

Board, R. G. and Halls, N. A. (1973b). Water uptake by eggs of mallards and guinea fowl. *Br. Poult. Sci.* **14**, 311-314.

Board, R. G. and Perrott, H. R. (1982). The fine structure of the outer surface of the incubated eggshells of the Helmeted guinea fowl (*Numidia meleagris*). *J. Zool.* **196**, 445-451.

Board, R. G. and Scott, V. D. (1980). Porosity of the Avian Eggshell. *Am. Zool.* **20**, 339-349.

Board, R. G., Tullett, S. G. and Perrott, H. R. (1977). An arbitrary classification of the pore systems in avian eggshells. *J. Zool.* **182**, 251-265.

Board, R. G., Perrott, H. R., Love, G. and Scott, V. D. (1984). The phosphate-rich cover on the eggshells of grebes (Aves: Podicipitiformes). *J. Zool.* **203**, 329-343.

D'Alba, L., Jones, D. N., Badawy, H. T., Eliason, C. M. and Shawkey, M. D. (2014). Antimicrobial properties of a nanostructured eggshell from a compost-nesting bird. *J. Exp. Biol.* **217**, 1116-1121.

D'Alba, L., Torres, R., Waterhouse, G. I. N., Eliason, C., Hauber, M. E. and Shawkey, M. D. (2017). What does the eggshell cuticle do? A functional comparison of avian eggshell cuticles. *Physiol. Biochem. Zool.* **90**, 588-599.

Deeming, D. C. (1987). Effect of cuticle removal on the water vapour conductance of egg shells of several species of domestic bird. *Br. Poult. Sci.* **28**, 231-237.

Deeming, D. C. (2002). *Avian Incubation: Behaviour, Environment and Evolution*. Oxford, UK: Oxford University Press.

Deeming, D. C. (2006). Ultrastructural and functional morphology of eggshells supports the idea that dinosaur eggs were incubated buried in a substrate. *Paleontology* **49**, 171-185.

Deeming, D. C. and Mainwaring, M. C. (2016). Functional properties of nests. In *Nests, Eggs and Incubation: New Ideas about Avian Reproduction* (ed. D. C. Deeming and S. J. Reynolds), pp. 29-49. Oxford, UK: Oxford University Press.

Deeming, D. C. and Reynolds, S. J. (2016). *Nests, Eggs and Incubation: New Ideas about Avian Reproduction*. Oxford, UK: Oxford University Press.

Ensikat, H. J., Ditsche-Kuru, P., Neinhuis, C. and Barthlott, W. (2011). Superhydrophobicity in perfection: the outstanding properties of the lotus leaf. *Beilstein J. Nanotechnol.* **2**, 152-161.

Fecheyr-Lippens, D. C., Igic, B., D'Alba, L., Hanley, D., Verdes, A., Holford, M., Waterhouse, G. I. N., Grim, T., Hauber, M. E. and Shawkey, M. D. (2015). The cuticle modulates ultraviolet reflectance of avian eggshells. *Biol. Open* **4**, 753-759.

Genzer, J. and Marmur, A. (2008). Biological and synthetic self-cleaning surfaces. *MRS Bull.* **33**, 742-746.

Gole, V. C., Chousalkar, K. K., Roberts, J. R., Sexton, M., May, D., Tan, J. and Kiermeier, A. (2014a). Effect of egg washing and correlation between eggshell characteristics and egg penetration by various *Salmonella typhimurium* strains. *PLoS ONE* **9**, e90987.

Gole, V. C., Roberts, J. R., Sexton, M., May, D., Kiermeier, A. and Chousalkar, K. K. (2014b). Effect of egg washing and correlation between cuticle and egg penetration by various *Salmonella* strains. *Int. J. Food Microbiol.* **182-183**, 18-25.

Hoyt, D. F., Board, R. G., Rahn, H. and Paganelli, C. V. (1979). The eggs of the Anatidae: conductance, pore structure, and metabolism. *Physiol. Zool.* **52**, 438-450.

Igic, B., Fecheyr-Lippens, D., Xiao, M., Chan, A., Hanley, D., Brennan, P. R. L., Grim, T., Waterhouse, G. I. N., Hauber, M. E. and Shawkey, M. D. (2015). A nanostructural basis for gloss of avian eggshells. *J. R. Soc. Interface* **12**, 20141210.

Ishikawa, S.-I., Suzuki, K., Fukuda, E., Arihara, K., Yamamoto, Y., Mukai, T. and Itoh, M. (2010). Photodynamic antimicrobial activity of avian eggshell pigments. *FEBS Lett.* **584**, 770-774.

Jaeckle, W. B., Kiefer, M., Childs, B., Harper, R. G., Rivers, J. W. and Peer, B. D. (2012). Comparison of eggshell porosity and estimated gas flux between the brown-headed cowbird and two common hosts. *J. Avian Biol.* **43**, 486-490.

Lahti, D. C. and Ardia, D. R. (2016). Shedding light on bird egg color: pigment as parasol and the dark car effect. *Am. Nat.* **187**, 547-563.

Lang, M. R. and Wells, J. W. (1987). A review of eggshell pigmentation. *World's Poultry Sci. J.* **43**, 238-246.

Manuwal, D. A., Carter, H. R., Zimmerman, T. S. and Orthmeyer, D. L. (2001). *Biology and conservation of the common murre in California, Oregon, Washington, and British Columbia. Vol. 1. Natural history and population trends*. US Geological Survey Biological Resources Division Information and Technology Report USGS/BRD/ITR-2000-0012, Washington, DC.

Maurer, G., Portugal, S. J. and Cassey, P. (2012). A comparison of indices and measured values of eggshell thickness of different shell regions using museum eggs of 230 European bird species. *Ibis* **154**, 714-724.

Maurer, G., Portugal, S. J., Hauber, M. E., Mikšík, I., Russell, D. G. D. and Cassey, P. (2015). First light for avian embryos: eggshell thickness and pigmentation mediate variation in development and UV exposure in wild bird eggs. *Funct. Ecol.* **29**, 209-218.

Mayani-Parás, F., Kilner, R. M., Stoddard, M. C., Rodríguez, C. and Drummond, H. (2015). Behaviorally induced camouflage: a new mechanism of Avian egg protection. *Am. Nat.* **186**, E91-E97.

Mikhailov, K. E. (1997). *Avian Eggshell: An Atlas of Scanning Electron Micrographs*. Hertfordshire, UK: British Ornithologists' Club Occasional Publications.

Nettleship, D. N. and Birkhead, T. R. (1985). *The Atlantic Alcidae: The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas*. London, UK: Academic Press Inc.

Portugal, S. J., Maurer, G. and Cassey, P. (2010). Eggshell permeability: a standard technique for determining interspecific rates of water vapor conductance. *Physiol. Biochem. Zool.* **83**, 1023-1031.

Portugal, S. J., Bowen, J. and Riehl, C. (2017). A rare mineral, vaterite, acts as a shock absorber in the eggshell of a communally nesting bird. *Ibis* **160**, 172-178.

Rahn, H. (1991). Why birds lay eggs. In *Egg Incubation: Its Effect on Embryonic Development in Birds and Reptiles* (ed. D. C. Deeming and M. W. J. Ferguson), pp. 345-360. Cambridge, UK: Cambridge University Press.

Rahn, H. and Paganelli, C. V. (1990). Gas fluxes in avian eggs: driving forces and the pathway for exchange. *Comp. Biochem. Physiol. A Physiol.* **95**, 1-15.

Rahn, H., Krog, J. and Mehlum, F. (1983). Microclimate of the nest and egg water loss of the Eider *Somateria mollissima* and other waterfowl in Spitsbergen. *Polar Res.* **1**, 171-183.

Rokitka, M. A. and Rahn, H. (1987). Regional differences in shell conductance and pore density of avian eggs. *Respir. Physiol.* **68**, 371-376.

Samiullah, S. and Roberts, J. R. (2014). The eggshell cuticle of the laying hen. *World's Poult. Sci. J.* **70**, 693-708.

Simkiss, K. (1986). Eggshell conductance—Fick's or Stefan's law? *Respir. Physiol.* **65**, 213-222.

Sparks, N. H. C. and Board, R. G. (1984). Cuticle, shell porosity and water uptake through Hens' eggshells. *Br. Poult. Sci.* **25**, 267-276.

Tazawa, H., Mikami, T. and Yoshimoto, C. (1971). Effect of reducing the shell area on the respiratory properties of chicken embryonic blood. *Respir. Physiol.* **13**, 352-360.

Thompson, M. B. and Goldie, K. N. (1990). Conductance and structure of eggs of Adelie penguins, *Pygoscelis adeliae*, and its implications for incubation. *Condor* **92**, 304-312.

Tøien, O., Paganelli, C. V., Rahn, H. and Johnson, R. R. (1988). Diffusive resistance of avian eggshell pores. *Respir. Physiol.* **74**, 345-354.

Tschanz, B. (1990). Adaptations for breeding in Atlantic Alcids. *Neth. J. Zool.* **40**, 688-710.

Tullett, S. G., Board, R. G., Love, G., Perrott, H. R. and Scott, V. D. (1976). Vaterite deposition during eggshell formation in the Cormorant, Gannet and Shag, and in 'Shell-less' eggs of the domestic fowl. *Acta Zool.* **57**, 79-87.

Tyler, C. (1969). The snapping strength of the egg shells of various orders of birds. *J. Zool.* **159**, 65-77.

Verbeek, N. A. M. (1984). The effects of adult fecal material on egg hatchability in Glaucous-winged Gulls (*Larus glaucescens*). *Auk* **101**, 824-829.

Vorobyev, A. Y. and Guo, C. (2015). Multifunctional surfaces produced by femtosecond laser pulses. *J. Appl. Phys.* **117**, 033103.

Wellman-Labadie, O., Picman, J. and Hincke, M. T. (2008). Antimicrobial activity of the Anseriform outer eggshell and cuticle. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **149**, 640-649.

Yuan, Y. and Lee, T. R. (2013). Contact angle and wetting properties. In *Surface Science Techniques* (ed. G. Bracco and B. Holst), pp. 3-34. Heidelberg, Berlin, Germany: Springer.

Zimmermann, K. and Hipfner, J. M. (2007). Egg size, eggshell porosity, and incubation period in the marine bird family Alcidae. *Auk* **124**, 307-315.

CHAPTER 7:

The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces

The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces

Birkhead, T. R., Thompson, J. E. and Montgomerie, R. (2018). The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *The Auk*, **135**, 1020-1032.

Original article can be found using the link below:

https://academic.oup.com/auk/article/135/4/1020/5149021

Supplementary Materials can be found using the link below:

https://datadryad.org/stash/dataset/doi:10.5061/dryad.gb90p1c

Chapter context and thesis author's contributions: In addition to the two novel adaptive explanations for the Common Guillemot's pyriform egg shape presented in **Chapter 5**, this chapter presents published work in Ibis proposing an additional novel adaptive explanation: the stability hypothesis. This published paper from The Auk examines the plausibility of this stability hypothesis using two novel experimental set-ups. Evidence presented in this chapter clearly demonstrates that increases in both egg elongation and pointedness results in greater stability on increasingly steep slopes. Whilst the experiments presented here were carried out using human participants, the published paper discusses how our findings are biologically realistic to the breeding situations observed in natural Common Guillemot colonies. Of all the hypotheses to explain the pyriform shape of guillemot *Uria* spp. eggs, the stability hypothesis has the strongest evidential support.

In this study, I contributed to the development of the stability hypothesis. I assisted with the collection of egg samples for the experimental fieldwork on Skomer Island (conducted under licence). I designed and built the equipment to perform the stability trials. Data collection and collation from stability trials was conducted by myself. All eggs were measured, photographed and run through automated 2D-image shape analysis software by myself and I undertook the initial analyses of this dataset before providing it to R. Montgomerie for final statistical analyses.

Co-authors' contributions: T.R. Birkhead, in part, developed the stability hypothesis for this manuscript. T.R. Birkhead also assisted with obtaining egg samples for the experiments during fieldwork on Skomer Island. T.R. Birkhead wrote the initial draft of the manuscript and subsequent contributions and suggestions for re-drafts were also made by R. Montgomerie. The final statistical analyses and figures presented in the published article were conducted by R. Montgomerie.

The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 135, 2018, pp. 1020–1032
DOI: 10.1642/AUK-18-38.1

RESEARCH ARTICLE

The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces

Tim R. Birkhead,[1]* Jamie E. Thompson,[1] and Robert Montgomerie[2]

[1] Department of Animal and Plant Sciences, University of Sheffield, Sheffield, United Kingdom
[2] Department of Biology, Queen's University, Kingston, Ontario, Canada
* Corresponding author: t.r.birkhead@sheffield.ac.uk

Submitted March 8, 2018; Accepted June 12, 2018; Published August 22, 2018

ABSTRACT

The adaptive significance of avian egg shape is a long-standing problem in biology. For many years, it was widely believed that the pyriform shape of the Common Murre (*Uria aalge*) egg allowed it to either "spin like a top" or "roll in an arc," thereby reducing its risk of rolling off the breeding ledge. There is no evidence in support of either mechanism. Two recent alternative hypotheses suggest that a pyriform egg confers mechanical strength and minimizes the risk of dirt contamination of the blunt end. We present a new hypothesis: that the Common Murre egg's pyriform shape confers stability on the breeding ledge, thus reducing the chance that it will begin to roll. We tested this hypothesis by measuring the stability of Common Murre and Razorbill (*Alca torda*) eggs of different shapes on slopes of 20°, 30°, and 40° above the horizontal. Common Murre eggs were more stable, and easier to stabilize, than the more elliptical Razorbill eggs. Within Common Murre eggs, more pyriform eggs were more stable. From a fitness perspective, the stability of the Common Murre egg on a slope seems likely to confer an advantage and thus may be a strong force of natural selection favoring the pyriform shape.

Keywords: egg shape, pyriform, Razorbill, sloping surfaces, stability

El huevo piriforme de *Uria aalge* es más estable en superficies inclinadas

RESUMEN

El significado adaptativo de la forma del huevo de las aves es un problema de larga data en biología. Por largo tiempo, se creyó ampliamente que la forma piriforme del huevo de *Uria aalge* le permitía ya sea 'girar como una tapa' o 'rodar en un arco', reduciendo de este modo el riesgo de salirse del lecho de cría. No hay evidencia que apoye ninguno de estos mecanismos. Dos hipótesis alternativas recientes sugieren que un huevo piriforme brinda robustez mecánica y minimiza el riesgo de contaminación con suciedad del extremo romo. Aquí, presentamos y evaluamos una nueva hipótesis: que la forma piriforme del huevo de *U. aalge* brinda estabilidad en el lecho de cría, por ende reduciendo la probabilidad de comenzar a rodar. Evaluamos esta hipótesis midiendo la estabilidad de los huevos de diferentes formas de *U. aalge* y *Alca torda* en pendientes de 20°, 30° y 40° por sobre la horizontal. Los huevos de *U. aalge* fueron más estables y más fáciles de estabilizar que los huevos más elípticos de *A. torda*, y entre los huevos de *U. aalge*, los huevos más piriformes fueron los más estables. Desde una perspectiva de la adecuación biológica, la estabilidad en pendiente del huevo de *U. aalge* parece conferir una ventaja y por ende ser una potente fuerza de selección natural a favor de la forma piriforme.

Palabras clave: Alca torda, estabilidad, forma del huevo, piriforme, superficies inclinadas

INTRODUCTION

The shapes of birds' eggs vary considerably among the 10,000 extant and recently extinct species, from almost spherical to ovate to bi-conical to pyriform (i.e. pear-like or pointed), and one of the most extreme is the pyriform egg of the Common Murre (*Uria aalge*; Birkhead 2017, Birkhead et al. 2017a, 2017b, Stoddard et al. 2017). The adaptive significance of this shape, and indeed of the shapes of all other birds' eggs, is unclear. In a wide-ranging comparative study of avian egg shape, Stoddard et al. (2017) suggested that "flight efficiency" and thus adaptations for flight have been "critical drivers of egg shape variation in birds," with species best adapted for high-powered flight producing more elongated, more asymmetric eggs. However, only 4% of the variation in egg shape across the ~1,400 species studied by Stoddard et al. (2017) is explained by the hand-wing index (their measure of "flight efficiency") analyzed in that study. An alternative hypothesis is that egg shape evolves in response to adult posture during incubation and the type of substrate on which eggs are incubated.

Until recently, it was widely believed that the adaptive significance of the Common Murre's pyriform egg shape had been established. The most popular idea was that, when knocked by a bird or blown by the wind, the pyriform egg would spin on its axis (Hewitson 1831, Morris 1856, Thomson 1923). However, as early as 1903, this effect was shown to be an artifact of testing empty museum eggshells; real eggs are too heavy to spin in this way without unreasonable force (Wade 1903). A second idea, proposed initially by Belopol'skii (1957; see also Tschanz et al. 1969), was that its pyriform shape allowed the Common Murre's egg to roll in an arc and, hence, be less likely to roll off the breeding ledge. This idea was (and still is) widely reported in the ornithological literature (Drent 1975, Gill 2007, Lovette and Fitzpatrick 2016) and the popular press. But extensive testing by Ingold (1980) provided little conclusive support for this hypothesis (see also Birkhead 2017, Birkhead et al. 2017a, 2017b).

In an earlier paper (Birkhead et al. 2017b), we suggested that the pyriform shape might (1) reduce the chance of shell breakage by dissipating the forces of any impact—like an adult landing or stepping on the egg—across a wider surface of the shell; or (2) help to keep the blunt pole of the egg (where the embryo's head and the air cell are located) relatively free from debris and fecal contamination, allowing the embryo to respire more efficiently, because that region of the egg has a relatively high density of pores. Empirical observations confirm that, among naturally incubated Common Murre eggs, fecal contamination of the eggshell is less likely at the blunt end of the egg (Birkhead et al. 2017b).

Here, we present and test a new hypothesis: that the Common Murre's pyriform egg is more stable on a sloping ledge, and easier for the parent to manipulate, than a more elliptical egg. Common Murres breed at high densities (typically 20 pairs m^{-2}, but up to 70 pairs m^{-2}) and thus gain protection from aerial predators such as gulls and corvids (Birkhead 1977). High-density breeding can be achieved only by birds being extremely flexible with regard to their individual breeding site (an area typically 10 cm in diameter), and this often means that Common Murres breed on sloping ledges. In studies of both Common Murres and Thick-billed Murres (*U. lomvia*), around half of all breeding sites were classified as sloping (Gaston and Nettleship 1981, Birkhead and Nettleship 1987). In neither of these studies was the angle of the slopes measured directly; instead it was judged by eye, from a distance (through a telescope or binoculars) without disturbing the birds. In Birkhead and Nettleship (1987), "sloping" was classified as $>15°$ above the horizontal.

Several other details are relevant here. Both Common and Thick-billed murres typically breed with no nest and with neighboring birds often in direct physical contact. Like the extinct Great Auk (*Pinguinus impennis*), which also produced a single pyriform egg (Bengtson 1984), both murres have a single, centrally located brood patch (Belopol'skii 1957, Bengtson 1984) and incubate in a semi-upright position, usually with their egg held between (but not on) the legs or feet, with the blunt end of the egg facing outward. In 44 of 56 (79%) incubating Common Murres on Skomer Island, Wales, UK, where at least one foot could be clearly seen, the egg was not resting on the webs. In the remaining 12 birds, the egg rested to some extent on the inner web. In no case was the egg resting fully on the web(s) (T. R. Birkhead et al. personal observation).

Murres almost never leave their egg unattended (Tschanz 1990, T. R. Birkhead et al. personal observation). When breeding on a sloping site, they almost always incubate facing upslope (Figure 1), with the blunt end of the egg oriented upslope. Among 116 sites on Skomer where there was a perceptible slope, the egg was oriented with its blunt end upslope in 109 cases (94%). This is likely an underestimate, given that eggs in other positions were easier to see (T. R. Birkhead et al. personal observation).

By contrast, the Razorbill (*Alca torda*), a close relative of the murres, breeds at lower densities and often on the same cliff ledges as murres, but not in contact with, or even very close to, other Razorbills or murres. Razorbills very rarely breed on sloping sites and they incubate in a horizontal posture, with the egg positioned under one wing, often resting on a bed of pebbles (Tschanz 1990, T. R. Birkhead et al. personal observation). They lay a single elliptical-ovate egg, but they have 2 brood patches—one on either side of their midline (Belopol'skii 1957). When breeding in crevices, Razorbills routinely leave their egg unattended, which would not be possible without the risk of the egg rolling out of place if they used sloping ledges (Tschanz 1990).

A murre egg is most vulnerable to rolling—especially on a sloping site—during the exchange of incubation duties, which takes place once or twice every 24 hr (e.g., Verspoor et al. 1987). At the end of each incubation bout, the incubating bird gently eases itself off its egg, leaving the egg at the site, even if the site is sloping. During the exchange, the egg is allowed to rest—albeit briefly—on the substrate with little or no assistance or support from either parent. This is not an issue for pairs breeding on horizontal sites (or for Razorbills), but it requires careful maneuvering and manipulation of the egg by murres breeding on sloping sites. These differences between the Razorbill and Common and Thick-billed murres suggest that the murres' pyriform egg shape may be an adaptation to breeding on sloping ledges.

METHODS

This study was conducted on Skomer Island in May–June 2017. Eggs were weighed (± 0.01 g), and their maximum

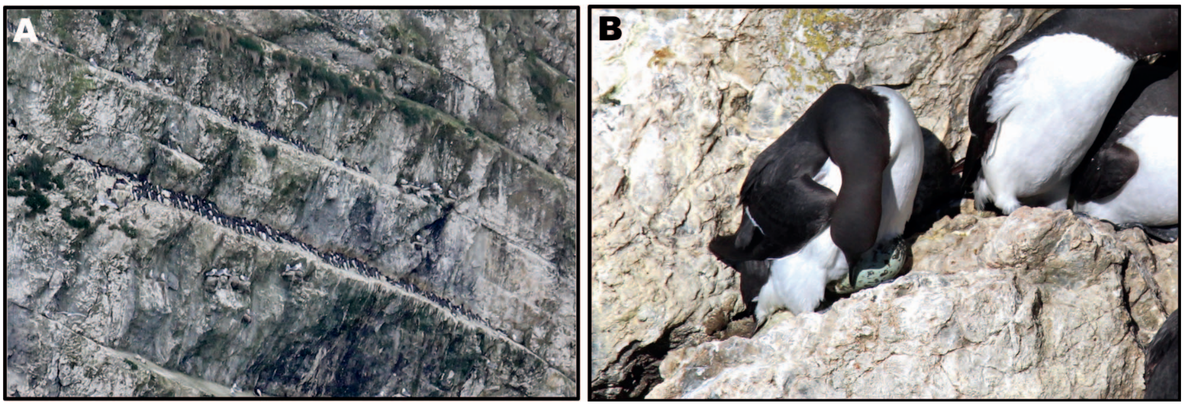


FIGURE 1. Common Murre breeding sites. (**A**) Part of the colony on a steep (30°) slope on Bempton Cliffs, Yorkshire, UK, showing that the majority of incubating birds are oriented with heads directed upslope. (**B**) An adult Common Murre on Skomer Island, Wales, UK, incubating its single egg, with the blunt end oriented away from the bird and upslope. Photo credit: T. R. Birkhead

length and breadth were measured (±0.1 mm) using vernier calipers. Each egg was scored as clean or dirty, with a dirty egg defined as one with enough dirt on it to obscure the smoothness of the outline.

We calculated the shape of each egg from photographs taken under standardized conditions. We have shown elsewhere (Biggins et al. 2018) that the shapes of birds' eggs, including the pyriform shape of Common Murre eggs, can be accurately quantified by 3 shape indices, described by Preston (1968, 1969), that we refer to as (1) pointedness, (2) elongation, and (3) polar asymmetry. Pointedness is the proportion of overall egg length that lies between the egg's widest point and its more pointed end. Elongation is the ratio of maximum length to maximum breadth. Polar asymmetry is determined by measuring the diameter of a circle at each end of the egg, such that each circle is the largest one that touches the respective pole of the egg but remains inside the outline of the eggshell. Polar asymmetry is the ratio of those diameters (large end: pointed end). Eggs with a relatively small pointed end have higher polar asymmetry values (Biggins et al. 2018).

Egg Stability Experiments

We tested the ability of recently laid eggs of different shapes to remain stable on 2 sloping surfaces, one moving and one static, in 2 experiments.

Experiment 1: Moving slope. One of us (J.E.T.) placed individual eggs on a horizontal platform covered with a 10 × 10 cm sheet of sandpaper on a motor-controlled slope such that the blunt end of the egg faced upslope (as it would during natural incubation). Slowly raising the slope of this surface at 4.5° s^{-1}, we recorded the angle above the horizontal at which the egg began to roll away from its original position. Tests were conducted with 38 Common Murre eggs ($n = 30$ clean, $n = 8$ dirty) and 10 Razorbill eggs.

We used a P120-grit aluminum oxide sandpaper substrate to simulate the friction that Common Murre eggs might experience on natural rocky breeding sites. P120 is the ISO/FEPA grit designation with an average particle diameter of 125 μm of abrading materials embedded in the sandpaper. We did not use smooth, uniform substrates because Common Murre breeding sites are rarely, if ever, like that. Instead, we used sandpaper (rather than rock) as a rough surface and humans (rather than Common Murres) as manipulators to standardize our experiments, recognizing that the actual surfaces that Common Murres breed on are more complex and irregular and that Common Murres would likely have considerably more difficulty stabilizing eggs than humans do. Thus, our experiments were not designed to perfectly mimic the natural situation, which would be extremely difficult. Our substrate (sandpaper) was rough but constant, and the egg manipulators (humans) were adept. Thus, the effects of slope on egg stability that we report are likely to be much stronger in nature, where substrates (rock) are more variable and the manipulators (Common Murres) much less likely to be able to stabilize the eggs.

Experiment 2: Static slope. Using information from experiment 1—which showed that almost all eggs were stable when the slope was <20° but that only a few were stable when the slope was increased to 40°—we created 3 slopes (20°, 30°, and 40°) using the same sandpaper substrate as above. J.E.T. attempted to position each egg stably on each slope within 10 s. Ten trials were conducted for each egg ($n = 59$ Common Murre, $n = 10$ Razorbill), and the number of successful attempts was recorded. Thirty-nine of the Common Murre eggs were clean and 20 were dirty. For the shape parameters of the eggs used in

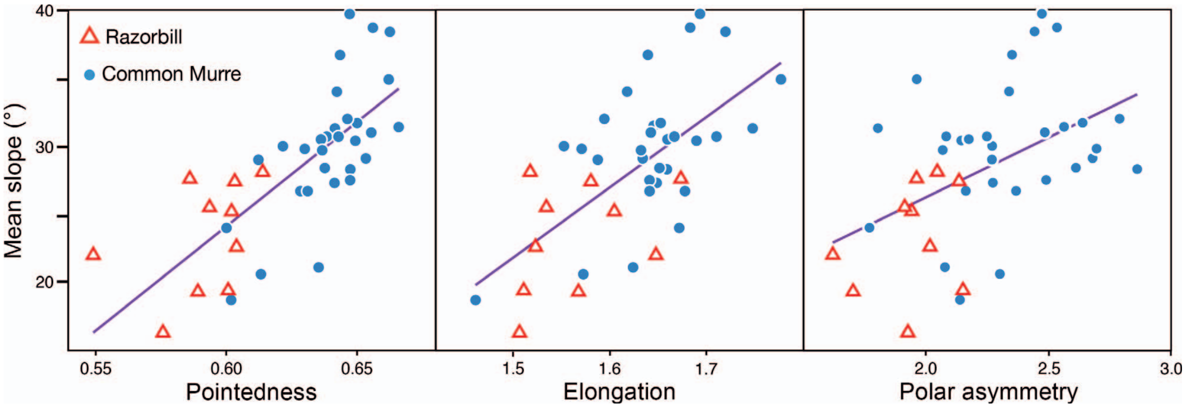


FIGURE 2. Stability of clean Razorbill ($n = 10$) and Common Murre ($n = 30$) eggs in relation to egg shape parameters, showing the mean slope at which each egg began to roll. Each point is the average of 5 measurements for each egg on a surface that slowly increased in slope. The regression is drawn through all the data because the species were not significantly different (see Appendix Table 6). These graphs do not control for the other variables in the best-fitting models (Table 1).

this experiment, see Appendix Figure 6 and Appendix Table 3.

Because the single observer in this experiment was not blind to the hypotheses being tested and thus was potentially biased, we repeated the experimental protocol using that single observer and 12 naive observers on a subset of the original eggs ($n = 2$ Razorbill, $n = 10$ Common Murre). There was no significant effect of potential bias on the success rates of stabilizing eggs of either species (generalized linear mixed models with binomial link, $P > 0.60$; see Appendix Table 4).

Slopes of Natural Breeding Sites

We measured the slope of the substrate on which 39 Common Murres and 23 Razorbills incubated on Skomer. To do this, we used a digital spirit level (Digi-Pas DWL-80E 0.1° resolution, 10 cm) attached to a 3D-printed Common Murre egg of average shape made of rigid nylon, such that when the egg had its maximum shell area (see Birkhead et al. 2017b) in contact with the substrate, the spirit level read zero.

Statistical Analyses

All analyses were performed using R 3.5.0 (R Core Team 2018). The full models we tested included egg mass and egg density (mass per unit volume) because both these variables might influence egg stability independent of egg shape. We reasoned that a heavier egg might make an egg more stable by increasing the friction against the substrate. We used density as a proxy for stage of incubation because Belopol'skii (1957) showed that the egg's center of gravity changes as incubation proceeds and that the mass of the egg of each species decreases by ~15% during the incubation period (Birkhead and Nettleship 1984).

We used Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham et al. 2011) to rank all models in each set and considered all models within 2 AIC$_c$ of the best-fitting model to be statistically equivalent, given the data. All continuous variables were standardized (mean = 0, SD = 1) so that the magnitudes of the estimates (std beta) could be directly compared. We report the best-fitting models below (for a summary of the top and averaged models in each set, see the Appendix).

RESULTS

Experiment 1: Increasing Slope Angle

On average, clean Common Murre eggs began to roll (i.e. become unstable) on higher slopes (30.0°, 95% confidence interval [CI]: 28.8–31.1) than clean Razorbill eggs 23.4° (95% CI: 21.7–25.0), a difference of 6.6° (linear model, $t = 5.9$, $P < 0.001$). However, despite this difference, the *relationships* between the mean slope at which a clean egg began to roll and each of the egg shape parameters were all positive (Figure 2) and did not differ significantly between the 2 species (Appendix Table 5). To establish whether the slope at which eggs began to roll was dependent on the mass and shape of eggs, we controlled for these 2 factors; as expected, the slopes at which clean Razorbill eggs (marginal mean = 27.7°, 95% CI: 23.1–32.2, $n = 10$) and Common Murre eggs (28.8°, 95% CI: 27.3–30.4, $n = 30$) began to roll did not differ significantly (Appendix Table 5), which confirms that the difference in the instability of eggs between these 2 species is due to their different size and shape.

Because 8 of the Common Murre eggs were dirty, we analyzed the species separately so that we could assess the effect of dirtiness on stability in that species. In the best-

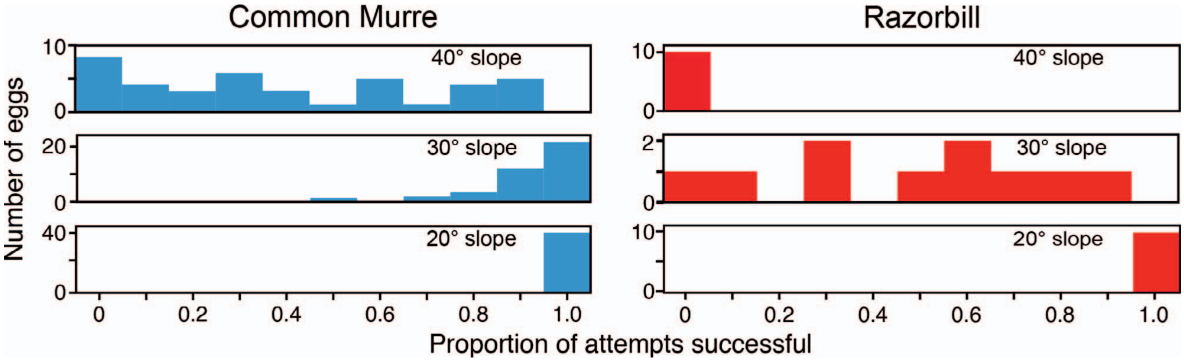


FIGURE 3. Stability of the clean eggs from 39 Common Murres and 10 Razorbills each tested on slopes of 20°, 30°, and 40° above the horizontal by a single observer. For each egg, the order of slopes on which it was tested was randomized, and each egg was tested 10 times on each slope to see whether it could be made stable within 10 s.

fitting models, pointedness was a significant predictor of the angle at which the egg began to roll in both Razorbills and Common Murres when the slope angle was gradually increased (Table 1). For Razorbills but not Common Murres, this model also included elongation, whereas for Common Murres the model also included egg density but that effect was not significant (Table 1). For both species, pointedness had the largest effect (std beta) on the angle that resulted in instability (Table 1). These best-fitting models predict 19–27% of the variation in the angle at which an egg began to roll (Table 1). Statistically equivalent models (top models, with $\mathrm{AIC_c} < 2$) added egg density as a predictor for Razorbill eggs, and elongation, polar asymmetry, and dirtiness as predictors for Common Murre eggs (see Appendix Table 7). Thus, egg shape influenced the stability of eggs of both species as the slope increased, with pointedness having the largest effect.

Experiment 2: Static Slope at Different Angles

It was possible to balance all 49 clean eggs of both species stably in every trial on 20° slopes, but none of the Razorbill eggs could be stabilized on the 40° slope (Figure 3). Thus, we focus our analyses on the results from experiments on 30° and 40° slopes, where there was variation in the ability to stabilize.

At both 30° and 40° slopes, Common Murre eggs were more likely to be stabilized than Razorbill eggs (Figure 3). For both species, the best-fitting models to predict stability contained elongation as a positive predictor (Table 2 and Figure 4). For Common Murre eggs on 40° slopes and Razorbill eggs on 30° slopes, pointedness was also included in the best-fitting models and had a larger effect (std beta) than elongation on the success of stabilizing. Also, for Common Murres, dirty eggs were easier to stabilize than clean ones on both 30° and 40° slopes (Table 2 and Figure 4). On the 40° slope, the ability to stabilize Common Murre eggs also increased significantly with egg density (Table 2 and Figure 4), presumably reflecting the increase in surface contact with the substrate as incubation advances. Statistically equivalent models (with $\mathrm{AIC_c} < 2$) for Common Murres added polar asymmetry as predictors on both 30° and 40° slopes, and both pointedness and egg density on 30° slopes (see Appendix Table 8).

We conclude from these analyses that egg shape influenced the stability of Common Murre and Razorbill eggs on sloped sites, with pointedness and elongation having the largest effects. In general, variation in polar asymmetry had little effect on the stability of eggs of either species, but dirty and more dense Common Murre eggs were easier to stabilize than clean ones on the steepest slope.

Slopes of Natural Breeding Sites

The slopes of Common Murre and Razorbill breeding sites on Skomer were clearly different, Common Murre sites

TABLE 1. Generalized linear mixed models to predict the angle at which an egg ($n = 10$ Razorbill, $n = 38$ Common Murre) began to roll as the slope of a rough surface was increased (std beta = magnitude of difference, CI = confidence interval). Predictors tested in the full model: egg shape parameters—pointedness (PT), elongation (EL), and polar asymmetry (PA)—as well as egg density (DE) and dirtiness (DT, Common Murres only). Best-fitting models are reported here (for top and averaged models, see Appendix Table 7). Each egg was measured on each slope, so egg identity was entered as a random effect in every model. Coefficients of multiple determination (R^2) calculated by the method of Nakagawa et al. (2017), which estimate the variance explained by both fixed and random effects.

Species	Predictor	Std beta (95% CI)	*F* (*P*)	R^2
Razorbill	PT	3.10 (1.25 to 4.95)	9.17 (0.02)	0.27
	EL	3.01 (1.16 to 4.86)	8.67 (0.02)	
Common Murre	PT	3.00 (1.84 to 4.28)	23.7 (<0.001)	0.19
	DE	−0.80 (−1.79 to 0.19)	1.59 (0.11)	

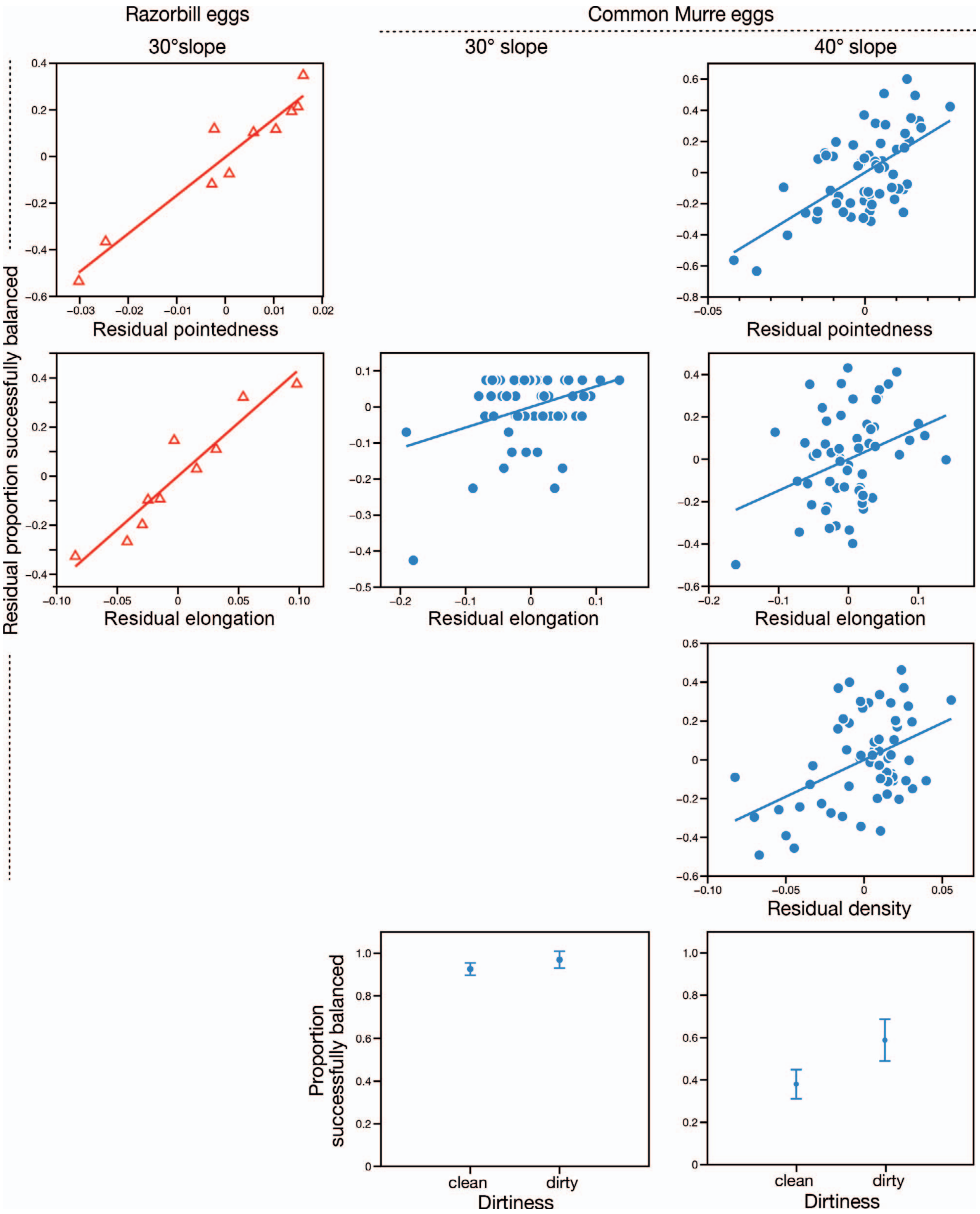


FIGURE 4. Partial regression plots of fixed effects for egg shape indices that significantly predict the success of stabilizing 10 Razorbill and 59 Common Murre eggs on different slopes (see Table 2). Plots for Common Murres also show the effects of dirtiness plotted as marginal means (± 95% confidence interval). These plots are from models whose predictors were not scaled, so that the magnitude of variation could be illustrated.

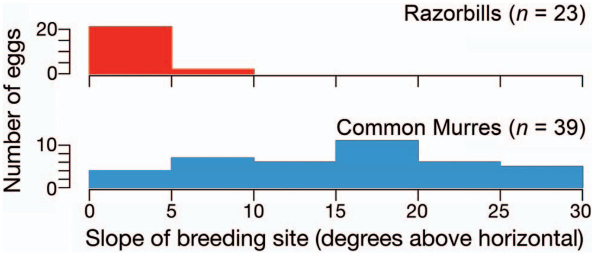


FIGURE 5. Slopes of ledges measured at breeding sites for 23 Razorbill and 39 Common Murre eggs on Skomer Island, Wales, UK.

being more sloping (median = 16.9°, range: 3.2–29.0°) than Razorbill sites (median = 1.3°, range: 0.3–6.9°; Mann-Whitney U-test, $W = 878.5$, $P < 0.001$), and the slopes of Common Murre sites were much more variable (Figure 5).

DISCUSSION

Our experiments demonstrate unequivocally that more pyriform (i.e. more pointed) eggs are more stable on sloping surfaces. We also show that, of our 3 egg shape indices, stability is primarily a consequence of pointedness and elongation. Given that pointedness also predicts the proportion of egg surface area in contact with the substrate (Birkhead et al. 2017b), the greater stability of pyriform eggs could be due in part to the friction resulting from the greater "contact area" that the narrow part of a pyriform egg has with the substrate.

It also seems likely that Common Murre eggs' center of gravity contributes to their stability, given that egg density positively affected stability on 40° slopes. Belopol'skii (1957) demonstrated that the angle at which a murre egg rests on the substrate changes through the course of incubation as the air cell (at the blunt pole) increases in size and the center of gravity shifts toward the pointed end of the egg. The result of this is that as incubation proceeds, the contact between the egg shell and the substrate increases. Belopols'kii (1957), who first proposed the rolling-in-an-arc explanation for the murre egg's pyriform shape, also noticed that the change in the center of gravity resulted in the egg rolling in a smaller arc and hence, he suggested, being less likely to fall from a ledge. However, we now know from Ingold's (1980) extensive experiments that neither the pyriform egg shape nor the shift in the center of gravity reduces the likelihood of the egg rolling off a ledge (see also Birkhead et al. 2017a, 2017b). Belopol'skii (1957) also interpreted the shift in the center of gravity as a murre-specific adaptation, although it is now known that the same change occurs in all birds' eggs during the course of incubation.

TABLE 2. Generalized linear models with binomial error to predict the number of trials out of 10 in which a Razorbill or Common Murre egg could be stabilized within 10 s by a single observer (std beta = magnitude of difference, CI = confidence interval). Best-fitting models are reported here (for top and averaged models, see Appendix Table 8); for Razorbills, there was only one top model. Each egg (n = 39 Common Murre, n = 10 Razorbill) was measured on each slope, so egg identity was entered as a random effect in every model. Predictors are the egg shape parameters pointedness (PT), elongation (EL), and polar asymmetry (PA), as well as egg density (DE). The coefficients of multiple determination (R^2) reported here estimate the proportion of variance explained by each model, following Nakagawa et al. (2017).

Slope, species	Predictor	Std beta (95% CI)	z (P)	R^2
30°, Razorbill	PT	1.64 (0.98–2.47)	4.40 (<0.001)	0.90
	EL	1.41 (0.76–2.19)	3.93 (<0.001)	
30°, Common Murre	DT	1.02 (0.18–2.03)	2.20 (0.03)	0.10
	EL	0.57 (0.25–0.89)	3.55 (<0.001)	
40°, Common Murre	DT	1.32 (0.83–1.82)	5.25 (<0.001)	0.70
	DE	0.75 (0.50–1.01)	5.78 (<0.001)	
	PT	1.17 (0.89–1.46)	8.10 (<0.001)	
	EL	0.52 (0.29–0.77)	4.23 (<0.001)	

Despite the apparent ubiquity and persistence of the spinning-like-a-top and rolling-in-an-arc "explanations" for the murre egg's pyriform shape, some previous authors have alluded to the stability conferred by this shape. For example, while not explicitly identifying the stability-on-a-slope hypothesis we present here, Pennant (1768:404) wrote: "What is also matter of great amazement, they [murres] fix their egg on the smooth rock, with so exact a balance, as to secure it from rolling off." Similarly, Macgillivray (1852:321) stated: "A very little inequality suffices to steady an egg [of a murre], and it is further prevented from rolling over by its pyriform shape."

Many Common Murres breed on approximately horizontal substrates, for obvious reasons, but as our data show, they are more likely than Razorbills to breed on sloping sites. In our study, the strongest stability effects were observed on slopes of 40°, yet our human subjects were undoubtedly much more dexterous and proficient using their hand to position an egg stably on a slope than a Common Murre would be using its beak, breast, legs, and wings. Our data indicate that few Common Murres breeding on Skomer use such steeply sloping sites, but our sampling was necessarily biased in this respect, precisely because our gaining access to such sites would probably result in the loss of eggs as the incubating bird left and, hence, the loss of our ability to identify them as breeding sites. On the other hand, visual inspection of sites without disturbing the birds (as in Gaston and Nettleship 1981, Birkhead and Nettleship 1987) does not indicate that breeding sites of 40° are common (Figure 1). Nonetheless, we suggest that the effect we have detected provides a meaningful index of the stability of an egg on sloping surfaces and the ability of the parent to manipulate and orient the egg for incubation on a sloping surface. The ability to keep an egg stable, especially during changeovers, provides Common Murres a flexibility in their choice of breeding site that allows them to achieve the high breeding densities necessary to provide protection from egg and chick predators like gulls.

We have shown elsewhere (Birkhead et al. 2017a) that egg shape in murres (of both species) is variable (but consistent within females), but no more so than in many other bird species that lay more-elliptical eggs. Nonetheless, the variation in murre egg shape raises the question of whether the birds "know" their own egg shape and select their breeding site accordingly.

The eggs of Great Auks and Thick-billed Murres are almost identical in shape but are slightly less pyriform than those of Common Murres (T. R. Birkhead et al. personal observation). How are these differences related to breeding on sloping sites? Thick-billed Murres are less "constrained" to breed at densities as high as those of Common Murres because they do not breed on broad ledges surrounded by conspecifics. Instead, Thick-billed Murres tend to breed predominantly on narrow ledges with no more than 1 or 2 neighbors (Birkhead and Nettleship 1987). This implies that they may have more flexibility regarding the type of site they use and may therefore not need to produce such a stable (pyriform) egg. A similar argument may apply to Great Auks, which also bred at high density (Montevecchi and Kirk 1996), but whether they bred as densely as Common Murres is not known. However, Great Auks' larger size would have provided better protection from predatory gulls and corvids, and it may therefore not have been as critical that they bred as densely as Common Murres. This, in turn, may have allowed them greater flexibility in their choice of breeding site.

In conclusion, the Common Murre's pyriform egg is both more stable and easier to stabilize on sloping surfaces than the more elliptical egg of the Razorbill. Among the Common Murre eggs that we tested, more pyriform eggs were also more stable. How do we rank this "stability hypothesis" with our 2 other hypotheses (Birkhead et al. 2017b), (1) minimizing egg shell breakage and (2) minimizing contamination at the blunt end? While not dismissing those 2 hypotheses (in part because they still require rigorous testing), we consider that the stability hypothesis provides a compelling additional reason why pyriform eggs might be favored by selection.

Because of the long and convoluted history of murre egg-shape explanations (see Birkhead 2017), there is a risk that our results will be misquoted or misinterpreted. To be clear, we do not dispute that the risk of the Common Murre's egg being lost from the breeding site is likely an important selection pressure on egg shape. Two mechanisms have previously been proposed to minimize the risk of murre eggs being lost from the breeding site—spinning like-a-top and rolling-in-an-arc—but neither is supported by the evidence. The spinning-like-a-top idea was based on the false assumption that the egg would spin on its axis when knocked or when blown by wind. The rolling-in-an-arc mechanism has been extensively tested but found not to be correct; in rolling tests, Ingold (1980) showed that a pyriform egg is no less likely to roll off a ledge than a Razorbill's more elliptical egg. Our new hypothesis—that pyriform eggs are more stable and easier to stabilize on a sloping surface—is supported by our experimental evidence. Increased stability would reduce the chance that an egg might roll away from the incubation site and off the ledge during incubation exchanges or when the adults flush in panic from the ledge when disturbed by a predator. Thus, we argue that the pyriform shape protects the Common Murre's egg by reducing the chance that it will roll, and not because it influences the rolling trajectory. Ease of stabilizing would also make incubation transfers between the parents safer and more efficient and would help the parents retrieve a slightly displaced egg.

ACKNOWLEDGMENTS

We thank the Wildlife Trust of South and West Wales (in particular, L. Wilberforce) for permission to work on Skomer Island. Thanks also to S. and A. Sutcliffe, various boatmen, and the wardens for their help on Skomer, to our student helpers who participated in the egg stabilization experiment, and to N. Hemmings, C. Holland, and J. Troscianko for useful comments on the manuscript.

Funding statement: The study was funded by grants from the Leverhulme Trust (to T.R.B.) and the Natural Sciences and Engineering Research Council of Canada (to R.M.).

Ethics statement: We are grateful to Natural Resources Wales for licenses to handle and photograph Common Murre and Razorbill eggs on Skomer Island.

Author contributions: T.R.B. conceived the idea. J.E.T. and T.R.B. developed the methods. J.E.T. performed the experiments. R.M. analyzed the data. T.R.B. and R.M. wrote the paper.

Data deposits: Data are deposited in Dryad (Birkhead et al. 2018).

LITERATURE CITED

Belopol'skii, L. O. (1957). Ecology of Sea Colony Birds of the Barents Sea. [Translated from the Russian, Israel Program for Scientific Translations, Jerusalem, 1961.]

Bengtson, S.-A. (1984). Breeding ecology and extinction of the Great Auk (*Pinguinus impennis*): Anecdotal evidence and conjectures. The Auk 101:1–12.

Biggins, J. D., J. E. Thompson, and T. R. Birkhead (2018). Accurately quantifying the shape of birds' eggs. Ecology and Evolution 8. In press.

Birkhead, T. R. (1977). The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). Journal of Animal Ecology 46:751–764.

Birkhead, T. R. (2017). Vulgar errors—the point of a guillemot's egg. British Birds 110:456–467.

Birkhead, T. R., and D. N. Nettleship (1984). Egg size, composition and offspring quality in some Alcidae (Aves: Charadriiformes). Journal of Zoology (London) 202:177–194.

Birkhead, T. R., and D. N. Nettleship (1987). Ecological relationships between Common Murres, *Uria aalge*, and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. II. Breeding success and site characteristics. Canadian Journal of Zoology 65:1630–1637.

Birkhead, T. R., J. E. Thompson, and J. D. Biggins (2017a). Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: Not a rolling matter? Journal of Ornithology 158:679–685.

Birkhead, T. R., J. E. Thompson, D. Jackson, and J. D. Biggins (2017b). The point of a guillemot's egg. Ibis 159:255–265.

Birkhead, T. R., J. E. Thompson, and R. Montgomerie (2018). Data from: The pyriform egg of the Common Murre *Uria aalge* is more stable on sloping surfaces. Dryad Digital Repository. doi:10.5061/dryad.gb90p1c

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Dormann, C. F., J. M. Calabrese, G. Guillera-Arroita, E. Matechou, V. Bahn, K. A. Bartoń, C. M. Beale, S. Ciuti, J. Elith, K. Gerstner, J. Guelat, et al. (2018). Model averaging in ecology: A review of Bayesian, information-theoretic and tactical approaches for predictive inference. Ecological Monographs. In press.

Drent, R. (1975). Incubation. Avian Biology 5:333–419.

Gaston, A. J., and D. N. Nettleship (1981). The Thick-billed Murres of Prince Leopold Island. Canadian Wildlife Service Monograph 6.

Gill, F. B. (2007). Ornithology, third edition. W.H. Freeman, New York, NY, USA.

Harris, M. P., S. Wanless, and T. R. Barton (1996). Site use and fidelity in the Common Guillemot *Uria aalge*. Ibis 138:399–404.

Hewitson, W. C. (1831). British Oology; Being Illustrations of the Eggs of British Birds. Empson, Newcastle upon Tyne, England.

Ingold, P. (1980). Anpassungen der Eier und des Brutverhaltens von Trottellummen (*Uria aalge aalge* Pont.) an das Brüten auf Felssimsen. Zeitschrift für Tierpsychologie 53:341–388.

Lovette, I. J., and J. W. Fitzpatrick (Editors) (2016). Handbook of Bird Biology, third edition. Wiley Blackwell, Hoboken, NJ, USA.

Luke, S. G. (2017). Evaluating significance in linear mixed-effects models in R. Behavior Research Methods 49:1494–1502.

Macgillivray, W. (1852). A History of British Birds, vol. 5: Cribratores, or Sifters; Urinatores, or Divers; Mersatores, or Plungers. William S. Orr, London, England.

Montevecchi, W A., and D. A. Kirk (1996). Great Auk (*Pinguinus impennis*), version 2.0. In Birds of North America Online (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.260

Morris, F. O. (1856). A History of British Birds. Groombridge, London, England.

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of the Royal Society Interface 14:20170213.

Pennant, T. (1768). British Zoology. Class I. Quadrupeds, II. Birds, Division II, Water Birds. Benjamin White, London, England.

Preston, F.W. (1968). The shapes of birds' eggs: Mathematical aspects. The Auk 85:454–463.

Preston, F. W. (1969). Shapes of birds' eggs: Extant North American families. The Auk 86:246–264.

R Core Team (2018). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Stoddard, M. C., E. H. Young, D. Akkaynak, C. Sheard, J. A. Tobias, and L. Mahadevan (2017). Avian egg shape: Form, function, and evolution. Science 356:1249–1254.

Thomson, A. L. (1923). Eggs. In The Pageant of Nature (M. P. Chalmers, Editor). Cassell, New York, NY, USA.

Tschanz, B. (1990). Adaptations for breeding in Atlantic alcids. Netherlands Journal of Zoology 40:688–710.

Tschanz, B., P. Ingold, and H. Lengacher (1969). Eiform und Bruterfolg bei Trottellummen, *Uria aalge aalge* Pont. Ornithologische Beobachter 66:25–42.

Verspoor, E., T. R. Birkhead, and D. N. Nettleship (1987). Incubation and brooding shift duration in the Common Murre, *Uria aalge*. Canadian Journal of Zoology 65:247–252.

Wade, E. W. (1903). The birds of Bempton cliffs. Transactions of the Hull Scientific and Field Naturalists' Club 3:1–26. [Reprinted as Wade, E. W. 1907. The Birds of Bempton Cliffs. A. Brown and Sons, London.]

APPENDIX

Here, we provide further details on the models and analyses reported in the text. The Statistical Supplement referred to below is archived in the Dryad Data Repository at doi: 10.5061/dryad.gb90p1c (Birkhead et al. 2018).

Statistical Analyses

In all models, continuous predictors were standardized so that the magnitudes of the estimates (std beta) can be directly compared, and the effect of each predictor is positive unless otherwise noted. Averaged models are calculated as the conditional average, as recommended by Dormann et al. (2018) when evaluating the effects of specific predictors, rather than using the model for prediction. We tested the significance of predictors in the linear mixed models using the Satterthwaite approximation (see Luke 2017).

Because sample sizes were relatively small, we limited the number of potential predictors in statistical models reported here and in the text. In the Statistical Supplement, we show more complex, but overparameterized, models that reach the same conclusions, as well as details of models presented here and tests of assumptions. Those more complex models suggest that interactions between egg parameters might also influence egg stability. While our results reported in this article show clearly that egg shape, density, and dirtiness influence the stability of Common Murre and Razorbill eggs on sloping surfaces, further research with larger sample sizes are needed to determine the effects of each egg shape parameter and their interactions.

Comparing Naive Observers to a Potentially Biased Observer

To evaluate the potential bias of the single observer who conducted experiment 2, we employed 12 observers (6 female and 6 male), naive to the purpose of the experiment, who were informed only that this was a test of their dexterity. Instead of using all eggs from experiment 2, we used a subset of those eggs consisting of 10 Common Murre eggs that spanned, as uniformly as possible, the range of egg shapes studied in that experiment, and 2 Razorbill eggs near the middle of the distribution of egg shapes from that species (Appendix Table 3 and Appendix Figure 6).

APPENDIX TABLE 3. Mean values of egg traits (with ranges in parentheses) for Razorbill and Common Murre eggs used in experiment 2 and in the procedure to determine whether the single observer in that experiment might have been biased. Egg mass and density both decreased slightly over the course of the experiment, so the descriptive statistics shown here are calculated from mean values per egg.

	Experiment 2, single potentially biased observer			Experiment 2, comparing observers	
		Common Murre			
Egg trait	Razorbill	Clean eggs	Dirty eggs	Razorbill	Common Murre
Sample size	10	39	20	2	10
Mass (g)	81.9 (67.7–91.1)	106.2 (91.6–116.9)	103.5 (91.6–119.7)	76.7 (73.9–79.6)	103.6 (93.2–111.8)
Density (g mL^{-1})	1.04 (1.00–1.08)	1.08 (1.00–1.11)	1.06 (0.99–1.11)	1.03 (1.02–1.04)	1.07 (1.06–1.08)
Pointedness	0.59 (0.55–0.61)	0.64 (0.60–0.67)	0.64 (0.61–0.67)	0.58 (0.55–0.61)	0.64 (0.60–0.67)
Elongation	1.57 (1.51–1.67)	1.64 (1.46–1.78)	1.64 (1.45–1.73)	1.58 (1.52–1.65)	1.65 (1.46–1.78)
Polar asymmetry	1.94 (1.6–2.15)	2.35 (1.77–3.06)	2.35 (1.90–2.93)	1.83 (1.62–2.05)	2.19 (1.77–2.64)

APPENDIX TABLE 4. Generalized linear mixed models with binomial error to predict the success of balancing 2 Razorbill or 10 Common Murre eggs on different slopes (20°, 30°, and 40° above horizontal) by different kinds of participants in the study: one potentially biased observer vs. 12 students blind to the hypothesis being tested. Participant identities, egg identities, and slopes were entered as random factors in each model to control for multiple measurements.

Species	Predictor	*z* (*P*)
Razorbill	Participant	0.64 (0.532)
Common Murre	Participant	0.74 (0.46)

APPENDIX TABLE 5. Linear models to predict the mean slope angle at which a clean egg (*n* = 30 Common Murre, *n* = 10 Razorbill) began to roll as the slope of a rough sandpaper surface was increased. Means were calculated for 5 measurements of each egg (CI = confidence interval). Separate models compared the 2 species for the different egg parameters without controlling for other variables in the models. Interaction terms between species and egg shape parameters were not significant ($P > 0.20$) and were removed from each model shown here.

Model	Response	Predictor	Estimate (95% CI)	*t* (*P*)	R^2
1	Mean slope angle	Pointedness	154.5 (109.3–199.7)	6.88 (<0.001)	0.51
2	Mean slope angle	Elongation	43.4 (24.9–62.0)	4.71 (<0.001)	0.33
3	Mean slope angle	Polar asymmetry	7.5 (2.7–12.3)	3.16 (0.003)	0.18

APPENDIX TABLE 6. Best-fitting generalized linear mixed model to predict the angle at which a clean egg began to roll as the slope of a rough sandpaper surface was increased (CI = confidence interval). This model compares species (clean eggs only: *n* = 30 Common Murre, *n* = 10 Razorbill) while controlling for egg mass, pointedness, and elongation, with egg identity as a random effect to control for multiple measurements of each egg. For all top models, see Statistical Supplement.

Predictors	Estimate (95% CI)	*F* (*P*)
Species	1.16 (−4.09 to 6.40)	0.17 (0.6)
Egg mass (g)	−1.32 (−3.05 to 0.41)	2.08 (0.16)
Pointedness	3.45 (1.86 to 5.05)	16.80 (0.0002)
Elongation	1.56 (0.40 to 2.72)	6.46 (0.01)

APPENDIX TABLE 7. Generalized linear mixed models for each species to predict the angle at which an egg (*n* = 38 Common Murre, *n* = 10 Razorbill) began to roll as the slope of a rough sandpaper surface was increased. Predictors tested in the full models were egg shape parameters—pointedness (PT), elongation (EL), and polar asymmetry (PA)—as well as egg density (DE, as a proxy for stage of incubation) and dirtiness (DT, scored as either clean [*n* = 30] or dirty [*n* = 8], for Common Murres only). Egg identity was included as a random effect to control for multiple measurements of each egg. (A) All top models ($\Delta AIC_c < 2$). (B) Averaged models calculated from those top models (std beta = magnitude of difference, CI = confidence interval, RVI = relative variable importance).

(A)

Species	Predictors	ΔAIC_c	Weight
Razorbill	PT, EL	0	0.57
	DE, PT, EL	1.52	0.27
Common Murre	−DE, PT	0	0.17
	PT	0.47	0.14
	−DE, PT, EL	0.49	0.14
	EL, PT	0.82	0.11
	−DE, PT, −PA	1.77	0.07
	DT, PT	1.94	0.07
	DT, DE, PT	1.97	0.06

(B)

Species	Predictor	Std beta (95% CI)	*z* (*P*)	RVI
Razorbill	EL	2.99 (1.29 to 4.69)	3.44 (<0.001)	1.0
	PT	3.17 (1.44 to 4.89)	3.60 (<0.001)	1.0
	DE	0.80 (−0.87 to 1.39)	1.03 (0.30)	0.32
Common Murre	PT	2.90 (1.57 to 4.23)	4.27 (<0.001)	1.0
	DE	−0.79 (−1.78 to 0.19)	1.57 (0.11)	0.58
	EL	0.90 (−0.45 to 2.24)	1.31 (0.19)	0.33
	DT	0.91 (−2.12 to 3.93)	0.59 (0.56)	0.17
	PA	−0.39 (−1.67 to 0.89)	0.60 (0.55)	0.09

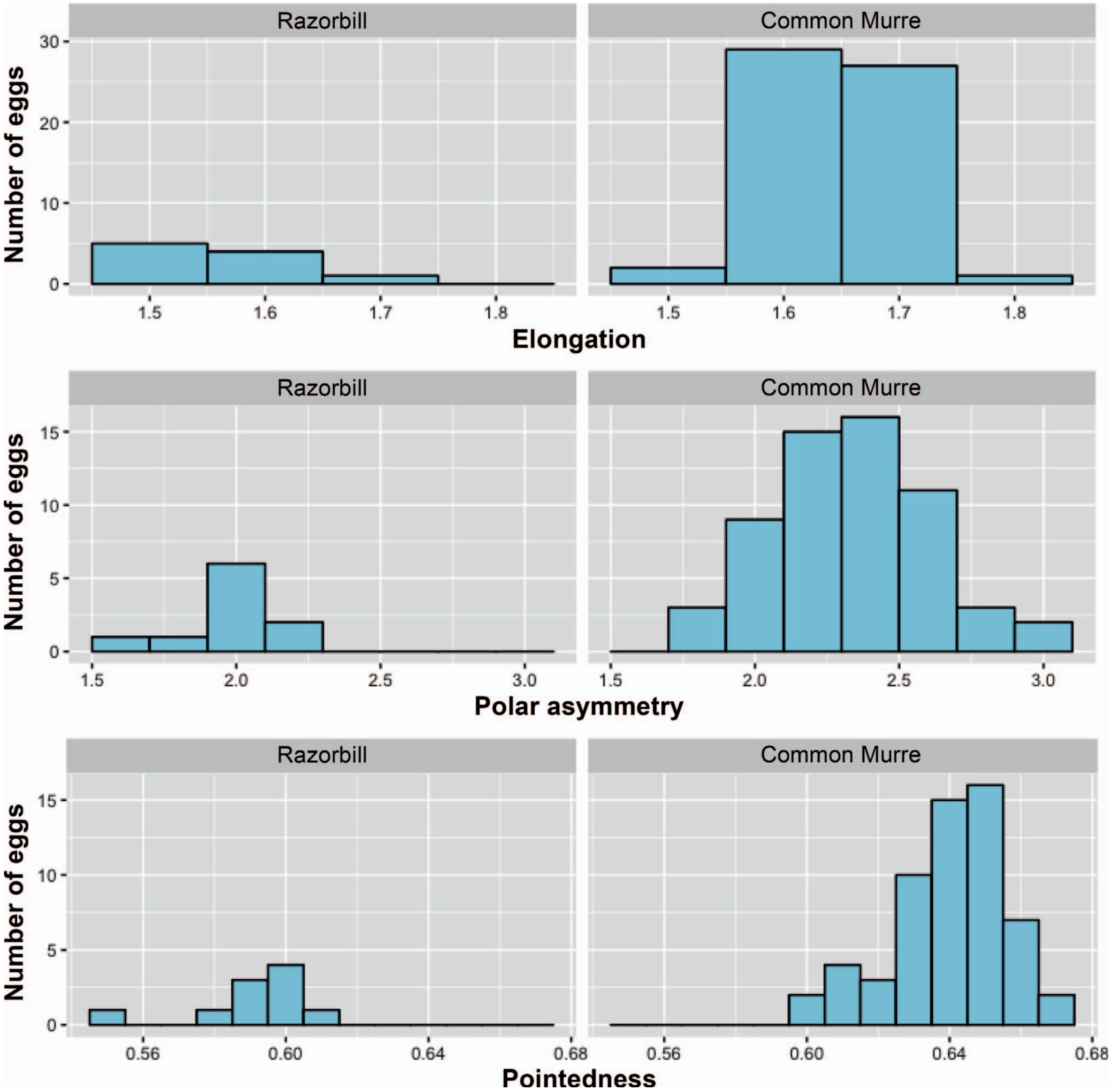
APPENDIX TABLE 8. Generalized linear mixed models with binomial error to predict the number of trials out of 10 in which an egg could be stabilized within 10 s by a single observer. Each egg ($n = 59$ Common Murre, $n = 10$ Razorbill) was measured on each slope. Predictors tested in the full model: egg shape parameters—pointedness (PT), elongation (EL), and polar asymmetry (PA)—as well as dirtiness (DT, scored as either clean or dirty), egg density (DE, for Common Murres only), and egg mass (MA). Egg identity was included as a random effect to control for multiple measurements of each egg. (A) All top models ($\Delta AIC_c < 2$) as determined using an information-theoretic approach to model evaluation. (B) Averaged models calculated from those top models (std beta = magnitude of difference, CI = confidence interval, RVI = relative variable importance).

(A)

Slope, species	Predictors	ΔAIC_c	Weight
30°, Razorbill	PT, EL	0	1
30°, Common Murre	DT, EL	0	0.10
	DT, −DE, EL	0.01	0.10
	DT, EL, PT	0.66	0.07
	−DE, EL	0.72	0.07
	DT, −DE, EL, PT	0.74	0.07
	−DE, EL, PT	0.81	0.06
	−DE, PT, −PA	1.27	0.05
	DT, −DE, PT, −PA	1.61	0.04
	−DE, EL, PT, −PA	1.82	0.04
40°, Common Murre	DT, DE, EL, PT	0	0.55
	DT, DE, EL, PT, −PA	1.29	0.29

(B)

Slope, species	Predictor	Std beta (95% CI)	*z* (*P*)	RVI
30°, Common Murre	EL	0.44 (0.04 to 0.85)	2.16 (0.03)	0.85
	DE	−0.40 (−0.88 to 0.07)	1.66 (0.10)	0.68
	DT	0.86 (−0.12 to 1.85)	1.71 (0.09)	0.65
	PT	0.39 (−0.10 to 0.88)	1.55 (0.12)	0.59
	PA	−0.29 (−0.71 to 0.12)	1.38 (0.17)	0.27
40°, Common Murre	DT	1.31 (0.81 to 1.81)	5.11 (<0.001)	1
	DE	0.76 (0.50 to 1.02)	5.68 (<0.001)	1
	EL	0.50 (0.25 to 0.76)	3.84 (0.001)	1
	PT	1.19 (0.89 to 1.50)	7.61 (<0.001)	1
	PA	−0.12 (−0.35 to 0.10)	1.07 (0.29)	0.34



APPENDIX FIGURE 6. Frequency distribution of egg shape parameters for the 59 Common Murre ($n = 39$ clean, $n = 20$ dirty) and 10 clean Razorbill eggs used in experiment 2.

CHAPTER 8:

The evolution of egg shape in birds: selection during the incubation period

The evolution of egg shape in birds: selection during the incubation period

Birkhead, T. R., Thompson, J. E., Biggins, J. D. and Montgomerie, R. (2019). The evolution of egg shape in birds: selection during the incubation period. *Ibis*, **161**, 605-618.

Original article and Supplementary Materials can be found using the link below:

https://onlinelibrary.wiley.com/doi/full/10.1111/ibi.12658

Chapter context and thesis author's contributions: Our studies of Common Guillemot egg shape (**Chapters 3-7**), strongly suggested that egg shape in this species has evolved in response to its unusual incubation situation. However, a broad comparative study by Stoddard et al. (2007) concluded that egg shape in birds had evolved as a response to flight efficiency rather incubation, and indeed they reported little to no effect of incubation on egg shape at a number of taxonomic scales. We tested the incubation hypothesis (i.e. that factors relating to incubation environment and/or behaviours act as significant drivers of egg shape) by comparing two taxa, auks and penguins, that exhibit extreme variation in egg shape and incubation situation and found clear evidence for an incubation effect on egg shape at broader taxonomic scales.

For the published work, I assisted with the development of ideas about incubation posture and its potential influence on egg shape. The measurement, photographing and automated shape analysis processing of over 1000 eggs for the manuscript's dataset was conducted by myself. I assisted with the collation and management of the dataset. I helped collate adult body mass measurements for the dataset and provided comments and improvements to re-drafts of the manuscript.

Co-authors' contributions: T.R. Birkhead and R. Montgomerie wrote the initial draft of the manuscript and provided improvements to subsequent re-drafts of the manuscript. Development of the idea about incubation posture and its potential influence on egg shape was, in part, developed by T.R. Birkhead. T.R. Birkhead assisted with the measurement of eggs. The collation and management of the dataset for the manuscript was, in part, conducted by R. Montgomerie. R. Montgomerie collated incubation site characteristics and some of the adult body mass information for the dataset. All final statistical analyses and figures in the published article were done by R. Montgomerie.

IBIS
BOU international journal of avian science
Ibis (2019), **161**, 605–618
doi: 10.1111/ibi.12658

The evolution of egg shape in birds: selection during the incubation period

TIM R. BIRKHEAD,[1]* JAMIE E. THOMPSON,[1] JOHN D. BIGGINS[2] & ROBERT MONTGOMERIE[3]
[1] *Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*
[2] *School of Mathematics and Statistics, University of Sheffield, Sheffield S3 7RH, UK*
[3] *Department of Biology, Queen's University, Kingston, ON, K7L 3N6, Canada*

A recent broad comparative study suggested that factors during egg formation – in particular 'flight efficiency', which explained only 4% of the interspecific variation – are the main forces of selection on the evolution of egg shape in birds. As an alternative, we tested whether selection during the incubation period might also influence egg shape in two taxa with a wide range of egg shapes, the alcids (Alcidae) and the penguins (Spheniscidae). To do this, we analysed data from 30 species of these two distantly related but ecologically similar bird families with egg shapes ranging from nearly spherical to the most pyriform eggs found in birds. The shape of pyriform eggs, in particular, has previously proven difficult to quantify. Using three egg-shape indices – pointedness, polar-asymmetry and elongation – that accurately describe the shapes of all birds' eggs, we examined the effects of egg size, chick developmental mode, clutch size and incubation site on egg shape. Linear models that include only these factors explained 70–85% of the variation in these egg-shape indices, with incubation site consistently explaining > 60% of the variation in shape. The five species of alcids and penguins that produce the most pyriform eggs all incubate in an upright posture on flat or sloping substrates, whereas species that incubate in a cup nest have more spherical eggs. We suggest that breeding sites and incubation posture influence the ability of parents to manipulate egg position, and thus selection acting during incubation may influence egg-shape variation across birds as a whole.

Keywords: alcids, auks, penguins, eggs, egg shape, incubation site, incubation posture, natural selection, evolution, birds.

The shapes of bird eggs vary considerably, from near-spherical in some owls to elongated and pyriform (pointed) in some waders, alcids and penguins (Hewitson 1831, Thompson 1917, Schoenwetter 1960–1992, Preston 1968, Deeming & Ruta 2014, Stoddard *et al.* 2017). Despite more than a century of interest, however, the physical causes and evolutionary explanations of interspecific differences in avian egg shape remain poorly understood (Deeming & Ruta 2014, Birkhead 2016, Stoddard *et al.* 2017). Egg shape also varies within species but this variation is generally small compared with that among even closely related species (Schoenwetter 1960–1992).

The different shapes of bird eggs have been given different names (e.g. Coues 1874, Romanoff & Romanoff 1949, Thomson 1964, Walters 1994), but there has never been an unambiguous definition of these shapes, and the usual categories grade into each other (see fig. S5 in Stoddard *et al.* 2017). Egg shape is also difficult to quantify and no single index accurately captures the full range of shapes across all bird species. Several authors have suggested that much of the interspecific variation in avian egg shape is captured by two indices – some measures of: (1) elongation (length relative to width), and (2) asymmetry (the extent to which the widest

*Corresponding author.
Email: t.r.birkhead@sheffield.ac.uk
Twitter: @bobmontgomerie

breadth of the egg deviates from the mid-point along the egg's length; Deeming & Ruta 2014, Stoddard *et al.* 2017).

A recent comparative study of avian egg shape by Stoddard *et al.* (2017) used publicly available (on the internet) photographs of 49 175 eggs of ~1400 species to calculate two indices of egg shape which they called 'ellipticity' and 'asymmetry', similar to elongation and asymmetry measured in other studies (see Biggins *et al.* 2018). Using those indices, they have made major contributions to the study of avian egg shapes by showing that: (1) there is continuous variation in shape across the Class Aves, with none of the discrete categories previously described, (2) egg shape is correlated with egg size across species, (3) extremely asymmetrical or extremely elliptical eggs are relatively rare, with the vast majority of species having eggs that are in the lower half of the range of each of their shape indices, and (4) the egg shape morphospaces (defined by a plot of ellipticity vs. asymmetry) occupied by different orders of birds overlap considerably, with no avian order having eggs that are absolutely distinctive. In addition, based on an earlier study by Mallock (1925), they present a biomechanical egg model that indicates that egg shape is plausibly determined by the structure of the shell membrane as it moves under pressure into the shell gland.

Using comparative analyses, Stoddard *et al.* (2017) reach the novel conclusion that the 'main driver' of interspecific variation in egg shape is 'flight efficiency' – bird species that are 'better' fliers have more elongated and more asymmetrical eggs. However, 'flight efficiency' measured as the hand-wing index (HWI) explained only ~4% of the total interspecific variation in egg shapes in their analysis of all species, suggesting that other factors are more likely to account for the broad pattern of interspecific variation in egg shape.

Although the broad comparative analysis presented by Stoddard *et al.* (2017) yields some interesting patterns, 40–50% of the variation in egg shape across the ~1400 species that they studied remains unexplained. The largest components of the explained variation in shape is due to egg size in relation to adult body mass (PC1 and 2), which accounted for 21% of the explained variation in asymmetry and 38.5% of the explained variation in ellipticity (see Stoddard *et al.* 2017: table S2B and C). Only 6.8–7.4% of the explained variation (thus about 4% of the total variation) was due to 'flight efficiency'.

One possible explanation for the large amount of unexplained variation in egg shape in those authors' analyses is that egg shape is influenced by different factors in different taxa. Stoddard *et al.* (2017) address that issue to some extent with separate analyses of seabirds, Passeriformes and Charadriiformes, although, even then, the unexplained variation in egg shape remains high at between 33 and 43%. As for the analyses of all species, most of the explained variation in shape is due to egg size in relation to adult body size (their PC1 and 2), and only 4.7–11.6% of the explained variation was accounted for by 'flight efficiency' (see Stoddard *et al.* 2017: tables S3B/C, S4B/C and S5B/C).

If some of that unexplained variation is due to unaccounted-for differences between taxa, then a focus on specific taxa with similar ecologies might improve our understanding of egg shape, and that is what we have done in this study. Our aim here is not to test the Stoddard *et al.* (2017) 'flight efficiency' hypothesis, but instead to present an alternative explanation for egg-shape variation in birds – that incubation is an important driver of avian egg shape. Birds incubate in such a wide variety of situations (with and without nests, for example), that selection for egg shape during the relatively lengthy incubation period seems much more plausible than during the brief (< 24-h) period of egg formation. In addition, previous studies have strongly implicated egg shape as an adaptation associated with incubation, such as to clutch size (Barta & Székely 1997), incubation efficiency (Andersson 1978), embryo respiration (Mao *et al.* 2007) and shell breakage (Juang *et al.* 2017).

Here we analysed egg shape in two distantly related bird families, the alcids (family Alcidae) and the penguins (family Spheniscidae), with similar lifestyles (i.e. strong submarine swimmers, flightless or weak fliers). The egg shapes in these two taxa alone occupy 40% of the morphospace of eggs measured by Stoddard *et al.* (2017), comprising > 55% of the range of 'ellipticity' and > 75% of the range of 'asymmetry' in their much larger sample of species (Fig. S6 in Appendix S4). Thus, the species we studied in the avian orders Charadriiformes and Sphenisciformes exhibit a larger range of egg shapes than is found in any other order of birds. Crucially, both of these taxa contain species with pyriform eggs, the one egg shape that Stoddard *et al.* (2017) were often unable to quantify accurately (see Biggins *et al.* 2018).

In this study, we obtained the three parameters necessary to quantify avian egg shape accurately from standardized digital photographs of individual eggs (Biggins *et al.* 2018), and examined the factors that might plausibly influence the shape of the eggs of 14 alcid and 16 penguin species.

METHODS

Hypotheses tested

We tested several hypotheses to explain interspecific variation in egg shape in the alcids and penguins, based on the results of research on other birds, as follows.

Egg size

Across birds, egg size increases with female body size (Huxley 1927, Rahn *et al.* 1975). Larger eggs tend also to be more elongated, even when controlling for female body size (Thompson 1917, Stoddard *et al.* 2017), possibly due to anatomical constraints on egg width (Deeming & Ruta 2014).

Developmental mode

Precocial chicks hatch from relatively larger eggs than altricial chicks, controlling for female size (Lack 1968, Ricklefs 1983). In a comparative study of a wide range of birds, Deeming (2018) also found that the eggs of species whose chicks are semi-precocial or precocial are more extreme in shape (both more elongated and more asymmetrical) than species producing altricial chicks (see also Stoddard *et al.* 2017 for evidence from the Charadriiformes).

Alcids are unique among birds in showing more variation in developmental mode than any other bird family – albeit all precocial to some degree – with chicks of different species classed as semi-precocial, 'intermediate' or precocial (Starck & Ricklefs 1998). In contrast, all species of penguins are semi-altricial (Williams 1995), so we cannot distinguish or control for the effects of phylogeny in our analyses with respect to developmental mode.

Clutch size

Within waterfowl (Rohwer 1988) in particular, and birds in general (Blackburn 1991), egg size decreases with clutch size, controlling for female size and other factors that influence egg size, such as developmental mode. Andersson (1978) modelled egg shape in relation to clutch size in waders and found that optimal egg shape for incubation varied with clutch size.

Breeding site

Several authors have suggested that the pyriform shape of the eggs of the *Uria* guillemots is an adaptation that minimizes damage during incubation on flat or sloping rock surfaces (MacGillivray 1852, Belopol'skii 1957, Tschanz *et al.* 1969, Ingold 1980, Birkhead *et al.* 2017b). Although the particular advantages of pyriform eggs are still debated, correlations between egg shape and (1) developmental mode and egg composition (Deeming 2018), (2) hatching success (Mao *et al.* 2007), and (3) shell damage (Juang *et al.* 2017) all suggest that egg shape might be influenced as much or more by selection during the incubation phase compared to factors that might affect shape during the relatively brief period of egg formation inside the female.

Material and data sources

Eggs were measured and photographed in museum collections (see Appendix S1 for further details) or under licence in the field (and a subset placed in a museum collection). We compiled female body masses for alcids from Gaston and Jones (1998) and Nettleship and Birkhead (1985), and for penguins from Williams (1995), Stein and Williams (2013) and Dehnhard *et al.* (2015). We compiled data on clutch sizes, developmental modes and incubation sites for each species from *Handbook of Birds of the World Alive* (del Hoyo *et al.* 2017) and *The Birds of North America* (Rodewald 2017). Developmental mode of the chicks was categorized as semi-altricial, semi-precocial, fully precocial and 'intermediate' (between fully precocial and semi-precocial), following Ricklefs (1983).

We attempted to obtain a minimum of five eggs per species to quantify shape. For three species (*Aethia cristatella*, *Alle alle*, *Spheniscus mendiculus*), however, we were not able to achieve that goal and so we analysed data with and without those species to ensure that those small samples of eggs were not biasing the shape indices in a way that would influence our conclusions.

We categorized incubation sites as being on bare rock, in crevices, in earth burrows, on the parent's feet or in cups (depressions often lined with vegetation). For phylogenies, we used Smith and Clarke (2015) for the auks, and Ksepka *et al.* (2006) for the penguins, both of which are consistent with recent phylogenies of birds from a wider variety of taxa (Jetz *et al.* 2012, Prum *et al.* 2015), although the lengths of branches were not quantified.

Measuring egg shape

Stoddard *et al.* (2017: Supporting Information) used Baker's (2002) method to quantify egg shape. However, as they point out, that method 'fails to provide a good fit for extremely pointy/asymmetric eggs'. As a result, they excluded from their analyses about 1300 (3%) of the eggs that they measured, mainly the more pyriform eggs (Stoddard *et al.* 2017: fig. S2). Previous researchers also recognized the difficulty of quantifying the pyriform shape of guillemot eggs (e.g. Thompson 1917).

Both Stoddard *et al.* (2017) and Deeming and Ruta (2014) relied on two egg-shape indices, essentially comprising 'elongation' (length relative to breadth) and 'asymmetry' (the relative position of the egg's widest point along its length) and which are often inadequate to quantify accurately the shapes of pyriform eggs. Preston (1968, 1969), however, identified three indices (elongation, asymmetry and bi-cone) to summarize the variation in the shape of all avian eggs (including pyriform eggs). These indices have not been widely used, probably for two reasons. First, two of his indices (bicone and asymmetry) depend on a measure of the curvature at each end of an egg, which he obtained from a specially constructed spherometer. Although it is possible to obtain these measures of curvature from photographs mathematically, this is computationally complex. Secondly, Preston's (1968) mathematical formulations may have deterred some researchers from using them. As a result, researchers have tended to use other methods to obtain indices of egg shape (see Deeming 2018).

The use of digital photography and new computational methods have made Preston's (1953, 1968, 1969; see also Todd & Smart 1984) methods more tractable (e.g. Birkhead *et al.* 2017a,b) and this is what we have used (see Biggins *et al.* 2018 for details). Our three indices of egg shape (see also Appendix S2) are:

- Pointedness (see Birkhead *et al.* 2017a,b): the proportion of overall egg length that lies between the egg's widest point and its more pointed end (the same as Deeming & Ruta's (2014) 'asymmetry ratio').
- Elongation: maximum length/maximum breadth. This is Preston's 'elongation', which is identical to the 'elongation ratio' of Deeming and Ruta (2014), and similar (but not identical) to Stoddard *et al.*'s (2017) 'tau', which they say is 'related to ellipticity'.
- Polar-asymmetry: the ratio of the diameters of the circles at opposite ends of the egg, such that each circle touches the pole of the egg and is the largest circle that remains inside the outline of the egg. This is broadly similar to Preston's (1968) 'asymmetry' except that he measured the eggs with a spherometer, whereas we used a mathematical model to calculate diameters from digital photographs. Eggs with a relatively small pointed end have higher values of polar-asymmetry and are in that sense more pyriform (Biggins *et al.* 2018).

Statistical analyses

For each shape index for each alcid and penguin species, we calculated the mean ± 95% confidence interval (CI) from a median of 10 (range 1–735) eggs per species using photographs taken under standardized conditions of eggs from 14 alcid and 16 penguin species (see Appendix S1). Our sample of alcid species includes the extinct Great Auk, whose eggs we were able to measure from published photographs (see Appendix S1 for details on this).

All statistical analyses were conducted in R version 3.5.0 (R Core Team 2018) and are summarized in Birkhead *et al.* (2018a) along with additional information about each model (e.g. tests of assumptions, model comparisons, parameter estimates, degrees of freedom). Continuous measurements (egg volume, egg length, egg breadth, female body mass) were $\log_{10}$-transformed to normalize distributions and simplify the interpretation of coefficients (see Appendix S3). To reduce the three egg measurements and three shape indices to a smaller set of orthogonal variables, we performed principal component analyses (PCAs) and report varimax-rotated components such that each variable loaded maximally on a single component axis (see Table S5 and Fig. S5 in Appendix S4).

For statistical analyses we constructed general linear models, testing model assumptions and transforming variables as needed to satisfy assumptions. We tested for interactions between some predictors, then omitted interaction terms with $P > 0.20$. Because our sample size of 30 species was relatively small, we constructed most models to predict each egg-shape index using three or fewer predictors, to minimize the effects of overparameterization. We used various combinations of predictors to assess the robustness of our conclusions (see Birkhead *et al.* 2018a).

We chose not to control for the effects of phylogeny in our main analyses but have done so, with an explanation, in Appendix S1. Controlling for phylogeny reveals the same patterns as described in the main text.

The R script, output and data files are all freely available online (Birkhead *et al.* 2018a).

RESULTS

Egg shape, egg size and body size

Female body mass alone accounts for 83% of the variation in egg volume in alcids and penguins (Table S1a in Appendix S4). Although the slopes of the relationships between egg volume and body mass did not differ between the alcids and penguins, alcid eggs are significantly larger for females of the same body mass (Table S1a in Appendix S1). The common slope (0.69, 95% CI 0.62–0.76) was significantly < 1 ($P < 0.0001$) indicating that, in both taxa, the eggs of the larger species are a smaller proportion of the adult female's body mass, as is broadly true across birds in general (Lack 1968).

Within both alcids and penguins, all three shape indices are positively correlated with egg size (Fig. 1, Table S1b in Appendix S4), and egg size and taxon together explain a large proportion of the variation in egg shape (41% of polar-asymmetry, 51% of pointedness, 76% of elongation; see Table S1c in Appendix S4). Controlling for variation in egg volume, alcid eggs are more elongated, more pointed and more asymmetrical than the penguin eggs, although there is considerable overlap with respect to pointedness and polar-asymmetry (Fig. 1). Although the three shape indices are correlated with one another ($r = 0.54–0.87$, $n = 30$ species, all $P < 0.002$; Fig. 2), in some cases all three are needed to describe the shape of the eggs in these taxa completely and accurately (see Biggins *et al.* 2018).

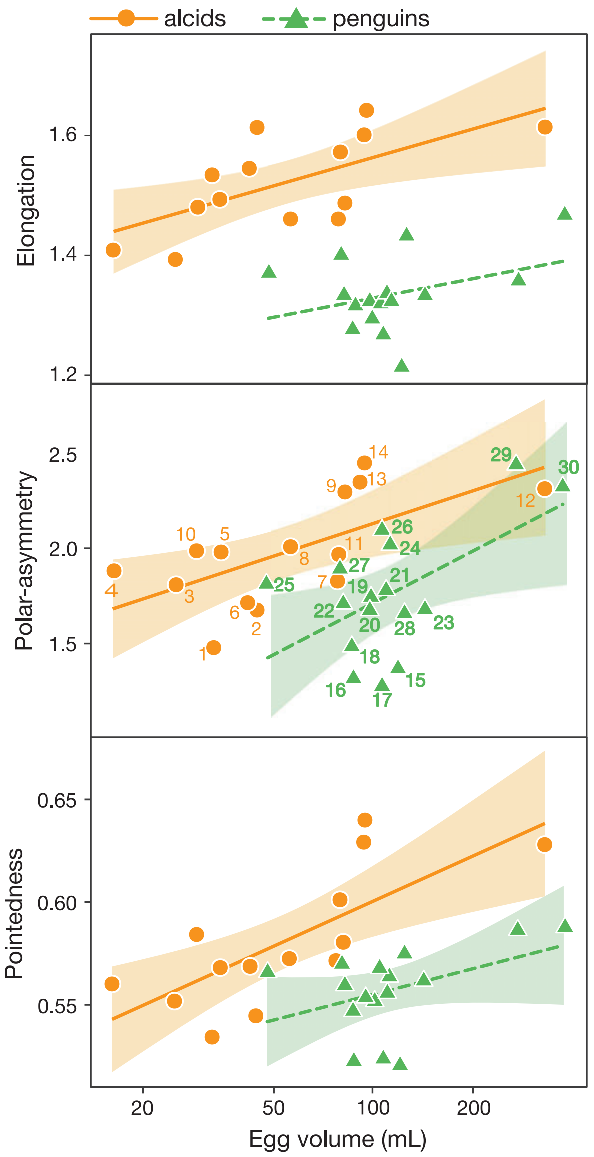


Figure 1. Relationships between egg-shape indices and egg volume in alcids and penguins. Regression lines are shown with 95% CI shaded. Species are: 1 – *Synthliboramphus wumizusume*, 2 – *Synthliboramphus antiquus*, 3 – *Ptychoramphus aleuticus*, 4 – *Aethia pusilla*, 5 – *Aethia cristatella*, 6 – *Cepphus grille*, 7 – *Cerorhinca monocerata*, 8 – *Fratercula arctica*, 9 – *Fratercula cirrhata*, 10 – *Alle alle*, 11 – *Alca torda*, 12 – *Pinguinus impennis*, 13 – *Uria lomvia*, 14 – *Uria aalge*, 15 – *Pygoscelis papua*, 16 – *Pygoscelis antarcticus*, 17 – *Eudyptes adeliae*, 18 – *Eudyptes moseleyi*, 19 – *Spheniscus demersus*, 20 – *Eudyptes pachyrhynchus*, 21 – *Spheniscus magellanicus*, 22 – *Eudyptes chrysocome*, 23 – *Eudyptes schlegeli*, 24 – *Spheniscus humboldti*, 25 – *Eudyptula minor*, 26 – *Megadyptes antipodes*, 27 – *Spheniscus mendiculus*, 28 – *Eudyptes sclateri*, 29 – *Aptenodytes patagonicus*, 30 – *Aptenodytes forsteri.* [Colour figure can be viewed at wileyonlinelibrary.com]

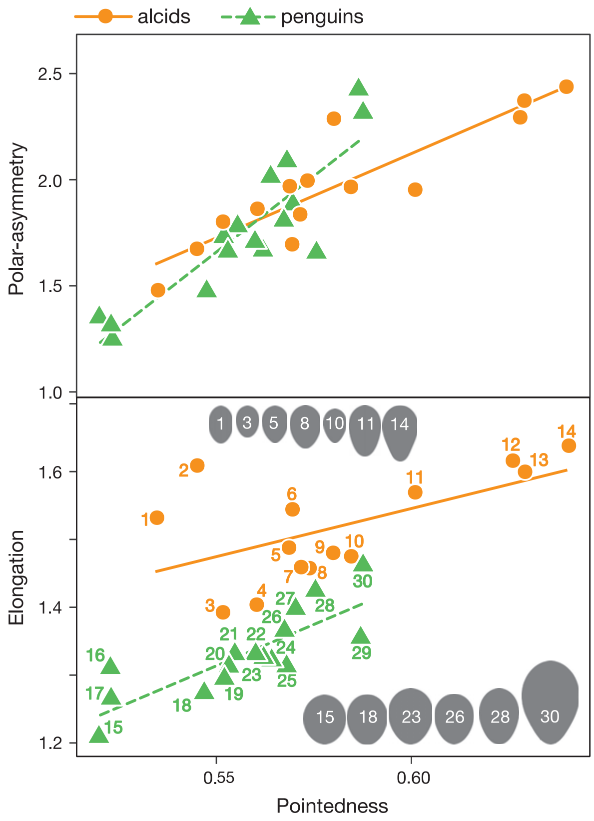


Figure 2. Relationships between different egg-shape indices in alcids and penguins. Regression lines are shown. Species are identified in Figure 1. Example silhouettes of the eggs of different species, to scale, show the range of variation in egg size and shape. [Colour figure can be viewed at wileyonlinelibrary.com]

Egg shape and developmental mode

The variation in egg volume in the alcids and penguins can be almost completely accounted for by interspecific variation in female mass and in chick developmental mode (Table 1, Fig. 3). For this reason we do not include female body mass in subsequent models.

Controlling for variation in egg volume, eggs producing semi-altricial chicks (i.e. all of the penguins) have significantly lower values for all three shape indices compared with the alcids producing semi-precocial and intermediate chicks (Fig. 4). Although there are some interesting general patterns here, there are also some anomalies of egg shape within each developmental mode. The Razorbill *Alca torda*, for example, has the same 'intermediate' developmental mode as the two *Uria* guillemots, but it produces a much less pyriform egg (less pointed, less asymmetrical) than the guillemots (Fig. 4b,c). In addition, alcids with the most precocial chicks (i.e. fully precocial category) have eggs that are the least asymmetrical and pointed (Fig. 4b,c), suggesting that the pyriform shape is not tightly linked with mode of development. As the developmental mode in all penguins is semi-altricial, the developmental hypothesis cannot explain the considerable variation in both polar-asymmetry and pointedness in this taxon (Fig. 4b,c). The range of polar-asymmetry in penguins, in fact, exceeds the entire range of polar asymmetries in the alcids (Fig. 4b), which are all precocial to some degree.

Table 1. Linear models to predict egg size and shape in 14 alcids and 16 penguins in relation to developmental mode (semi-altricial, semi-precocial, intermediate, precocial).

Response	Predictors	*F*	*P*
Egg volume	Developmental mode	29.8	< 0.0001
($R^2 = 0.96$)	Female body mass	298.8	< 0.0001
Pointedness	Developmental mode	19.3	< 0.0001
($R^2 = 0.72$)	Egg volume	4.7	0.04
Polar-asymmetry	Developmental mode	6.2	0.003
($R^2 = 0.48$)	Egg volume	7.0	0.01
Elongation	Developmental mode	39.2	< 0.0001
($R^2 = 0.84$)	Egg volume	4.1	0.08

The model predicting egg volume controls for female body mass, whereas the models predicting egg-shape indices control for egg volume. Both egg volume and female body mass are $\log_{10}$-transformed.

The consistent difference between alcids and penguins with respect to general developmental mode (altricial vs. precocial, respectively) accounts for the same amount of variation (96%) in egg volume, controlling for female body mass, as the analysis with more narrowly defined developmental modes (Table S2, Fig. S4 in Appendix S4). Thus we pooled all of the precocial modes (semi-precocial, intermediate, fully precocial) in subsequent analyses to reduce the effects of overparameterization. Comparing just those two general developmental modes, eggs with precocial chicks had significantly higher pointedness, elongation and polar-asymmetry (Fig. 5a,b,c; Table S2 in Appendix S4).

Egg shape and clutch size

There are only two different clutch sizes in the alcids and penguins, with each species typically

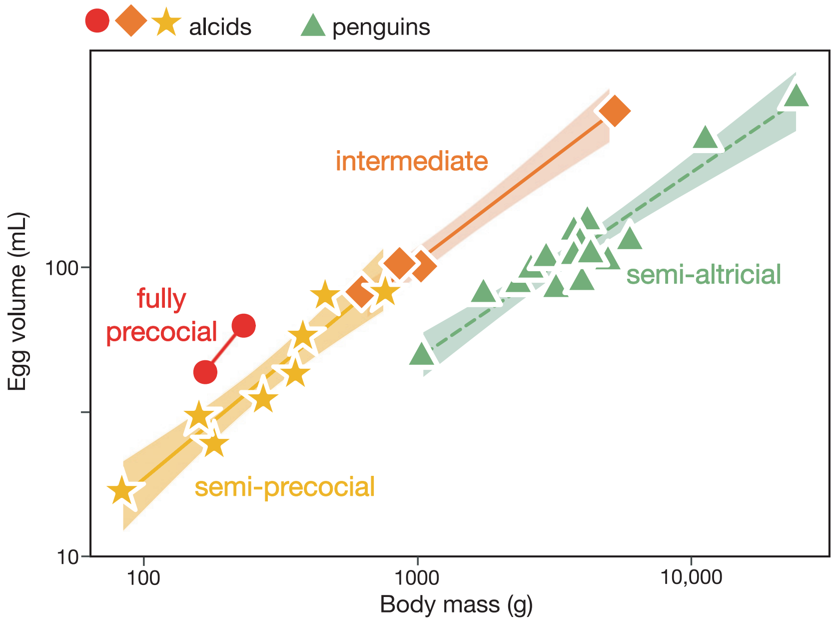


Figure 3. Relationship between egg volume and adult body mass (both $\log_{10}$-transformed) for alcids and penguins with different developmental modes. [Colour figure can be viewed at wileyonlinelibrary.com]

laying either one or two eggs and having either one or two incubation patches. Some alcids that lay single-egg clutches have two brood patches, but all of the species that lay two eggs have two brood patches. Species with single egg clutches have eggs that are more pointed and have a higher polar-asymmetry (Fig. 5e), controlling for egg volume and general developmental mode. Adding clutch size to the models predicting egg-shape indices had a substantial effect only on the model predicting polar-asymmetry, increasing the (adjusted) variance explained from 37 to 56% (Tables S2 and S3 in Appendix S4).

Egg shape and incubation site

To create a model for egg shape in relation to incubation site, we included egg size, clutch size and developmental mode as predictors, as they all had a significant effect on egg shape in some of the models reported above. All three egg-shape indices varied significantly with incubation site (Table 2), with a few large and statistically significant differences between site categories (Fig. 5g–i). For example, eggs laid on bare rock surfaces were significantly more pointed than those incubated in burrows or cups or on the parent's feet (Fig. 5i), and are significantly more elongated and asymmetrical than those incubated in cups, controlling for egg volume, clutch size and developmental mode (Fig. 5g,h).

Overall, models that included egg size, developmental mode, clutch size and incubation site explained 75–86% of the variation in the three egg-shape indices in these two taxa (Table 2). Models that included only incubation site as a predictor explained more than 65% of the variation in our separate egg-shape indices (66% of elongation, 66% of polar-asymmetry, 70% of pointedness; Table S4b in Appendix S4).

To further explore the relationship between egg shape and developmental mode, clutch size and incubation site, we used PCA to summarize egg size (volume, length, breadth) and our three size indices into two orthogonal variables. The first rotated component (RC1) explained 51% of the interspecific variation in egg size and shape and was strongly correlated with the three size variables (all loadings > 0.95). RC2 explained an additional 41% of the variation and was strongly correlated with the three egg-shape indices (all loadings > 0.86). Thus, the first two rotated components explained 92% of the interspecific variation. Egg size is positively correlated with RC1, whereas egg shape (pointedness, polar-asymmetry and elongation) is positively correlated with RC2

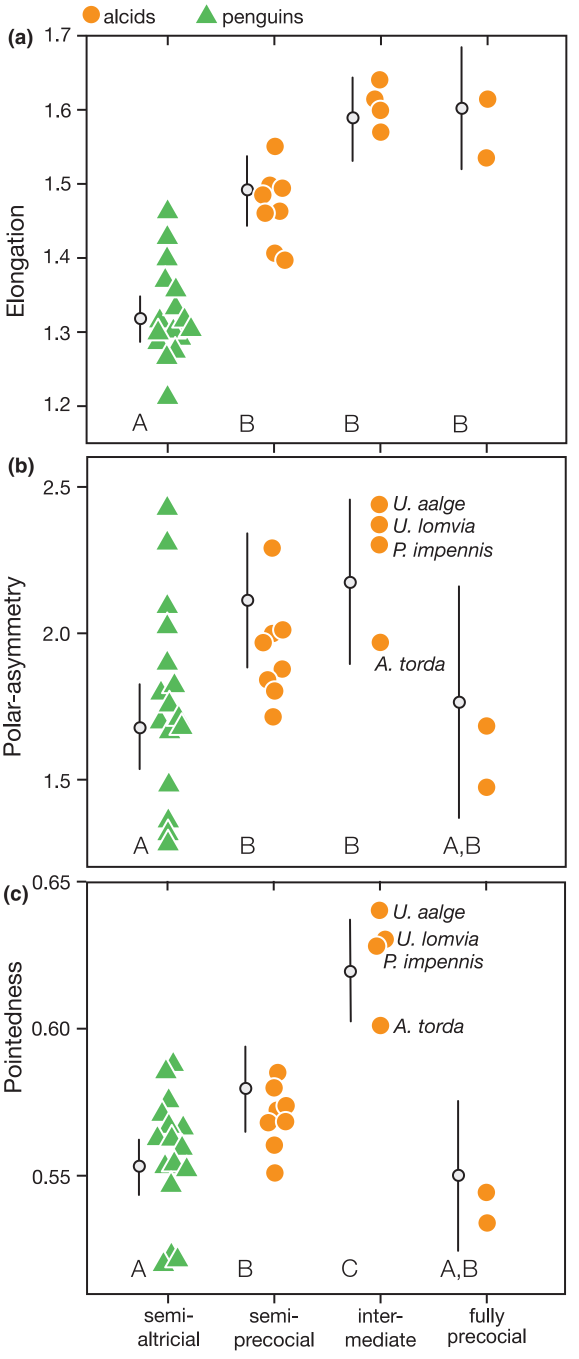


Figure 4. Relatiosnhip between egg-shape indices and chick developmental mode. Each panel shows the results of a different linear model, controlling for the effects of egg volume (see Table S2 in Appendix S4). Raw data are shown as filled symbols to the right of marginal means ± 95% CI from those linear models. Four species mentioned in the text are identified. Marginal means that are significantly different (Tukey contrasts) within each panel are identified by different letters above the *x*-axis. [Colour figure can be viewed at wileyonlinelibrary.com]

such that higher values of RC2 indicate a more pyriform shape.

Egg shape (RC2) varied significantly with incubation site, with eggs incubated on bare rock significantly more pyriform than those incubated in cups, crevices or burrows, and eggs incubated in cups significantly more elliptical (less pyriform) than those incubated in crevices or on rock (Fig. 6). This model explained 82% of the variation in egg shape (Table 2; see also Table S8 in Appendix S4). Removing the three species with fewer than five eggs measured had no effect on the results (Table 2).

Controlling for phylogeny, egg shape (RC2) remained significantly influenced by incubation site alone, in a best-fitting model controlling for clutch size (see Fig. S2 and Table S9 in Appendices S3 and S4). Thus eggs incubated on rock are significantly more pyriform than eggs incubated in burrows, and the rank order of effects (rock > feet > crevice > burrow > cup) is the same as when phylogeny is not controlled for (Fig. 6).

DISCUSSION

Between 75 and 86% of the variation in the shapes of alcid and penguin eggs is explained by clutch size and incubation site, controlling for variation in egg size (Table 2). Our results suggest that factors during the incubation period are largely responsible for selection on egg shape in these two taxa. This finding is consistent with previous work on the shapes of wader eggs (Andersson 1978), which also suggested that the optimal shape of those eggs was a function of selection for incubation efficiency, a factor that is relevant only after the eggs are laid.

Our analyses are quite different from those of the large-scale comparative study by Stoddard *et al.* (2017) in three important ways. First, we focused on only 30 species in two relatively small but unrelated taxa with similar ecologies, whereas Stoddard *et al.* (2017) studied the eggs of ~1400 species across the full range of bird diversity.

Secondly, we measured eggs photographed under standardized conditions, using a method that provided accurate shape indices for all avian eggs from the digitized images. As we show elsewhere, failure to standardize photos can lead to directional biases in the indices of some egg shapes

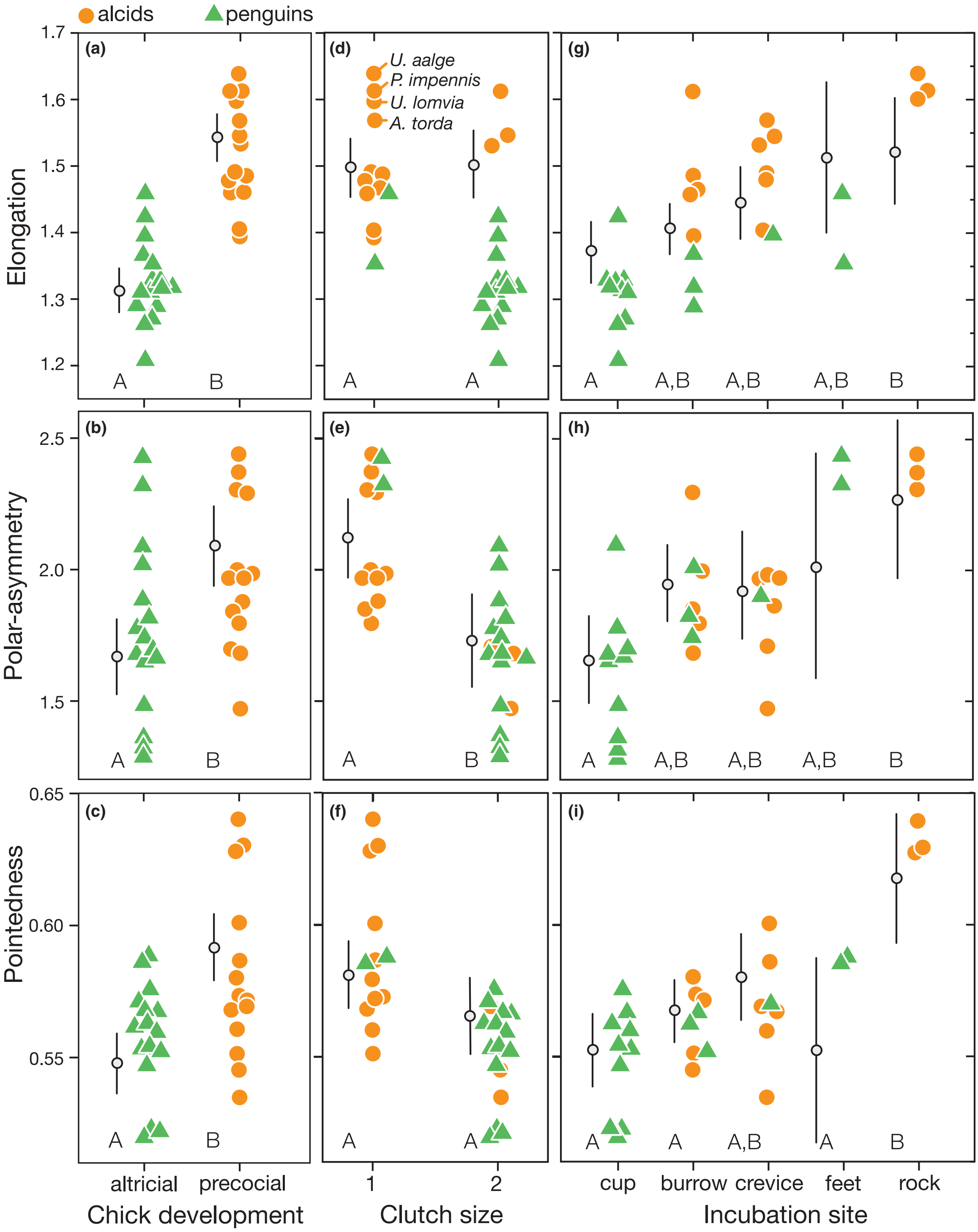


Figure 5. Relationship between egg-shape indices and general developmental mode (a,b,c), clutch size (d,e,f) controlling for general developmental mode, and incubation site (g,h,i) controlling for both general developmental mode and clutch size. Each panel shows the results of a different linear model, controlling for the effects of egg volume (see Tables S2, S3 and S4 in Appendix S4). Raw data are shown as filled symbols to the right of marginal means ± 95% CI from those linear models. Four species mentioned in the text are identified. Marginal means that are significantly different (Tukey contrasts) within each panel are identified by different letters above the *x*-axis. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 2. Linear models to predict egg-shape indices in alcids and penguins.

Response	Predictors	F	P
Polar-asymmetry (n = 14 alcids, 16 penguins) R^2 = 0.75	General developmental mode	1.5	0.24
	Egg volume	0.7	0.42
	Clutch size	6.9	0.02
	Incubation site	3.0	0.04
Pointedness (n = 14 alcids, 16 penguins) R^2 = 0.75	General developmental mode	0.6	0.44
	Egg volume	2.7	0.12
	Clutch size	5.9	0.02
	Incubation site	5.6	0.003
Elongation (n = 14 alcids, 16 penguins) R^2 = 0.86	General developmental mode	30.5	< 0.0001
	Egg volume	3.3	0.08
	Clutch size	7.4	0.01
	Incubation site	3.4	0.03
RC2 egg shape (n = 14 alcids, 16 penguins) R^2 = 0.82	General developmental mode	1.3	0.27
	Egg volume	1.2	0.28
	Clutch size	1.2	0.29
	Incubation site	4.4	0.009
RC2 egg shape (n = 12 alcids, 15 penguins) R^2 = 0.81	General developmental mode	1.5	0.23
	Egg volume	0.8	0.38
	Clutch size	0.6	0.44
	Incubation site	4.0	0.02

The general egg-shape index (RC2) is calculated from PCA of the egg shape and size variables. RC2 is modelled with both the full dataset and a dataset without three species for which we had measured fewer than five eggs. RC2 was recalculated for the analysis of the reduced dataset. See also Tables S2, S3, S7 and S8 in Appendix S4.

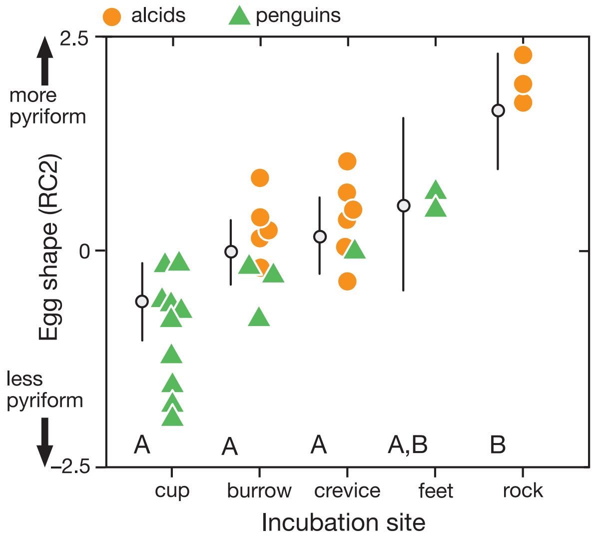


Figure 6. Relationship between a general egg-shape index (RC2) and incubation site, controlling for both general developmental mode and clutch size (see also Table S7 in Appendix S4). Raw data are shown as filled symbols to the right of marginal means ± 95% CI from the linear model. Marginal means that are significantly different (Tukey contrasts) within each panel are identified by different letters above the x-axis. [Colour figure can be viewed at wileyonlinelibrary.com]

and adds to noise (unexplained variation) in the indices of all egg shapes (Biggins *et al.* 2018).

Thirdly, we did not consider any measure of 'flight efficiency' because our aim was not to test the hypothesis of Stoddard *et al.* (2017), and we felt that the analysis of HWI was unlikely to be revealing for reasons given below.

Elongation and asymmetry as a way of making larger eggs

In the alcids and penguins – as in birds in general (Stoddard *et al.* 2017, Deeming 2018) – larger eggs tend to be more elongated and more asymmetrical. Increasing elongation is one way of increasing egg volume without increasing egg width, suggesting that egg width is constrained in birds in general, as most species lay elongated rather than spherical eggs. However, in contrast to mammals (and dinosaurs), where neonatal embryo size is constrained by the dimensions of the pelvic opening, birds have an incomplete pelvis (Dyke & Kaiser 2010, Deeming & Mayr 2018) and so this skeletal constraint does not exist to the same extent, as is strikingly demonstrated by (1) the capacity of some species (e.g. *U. aalge*) to lay large double-yolked eggs (see Birkhead *et al.* 2017a), and (2) those alcids with fully precocial development that produce relatively large and elongated eggs compared with the eggs of the semi-altricial penguins. Instead, egg width in birds might be more constrained by the ability of the oviduct to stretch. It is not clear why there has been selection for asymmetry in species that lay larger eggs, unless there is some associated benefit to the egg or the female during the incubation phase, as we propose below.

Developmental mode

Deeming (2018) convincingly suggests that developmental mode (or some correlate of it, such as relative egg size) plays a role in egg shape (see also Stoddard *et al.* 2017: table S5B and fig. S15). Yet, across all bird species, precocial and semi-precocial chicks develop from both pyriform and non-pyriform eggs. Thus, a more pyriform egg may be an adaptation to specific circumstances during the incubation period, as we suggest for alcids and penguins.

Incubation site and female posture

The two guillemots (*Uria* spp.) and the two penguins (*Aptenodytes* spp.) that produce the most pyriform eggs all incubate in an upright posture. This was probably also true of the Great Auk (Bengtson 1984). Both of the *Uria* guillemots nest in dense colonies on rock ledges in the polar north (Gaston & Jones 1998), whereas the two penguins nest in dense colonies on soil, rock and ice in the polar south (Williams 1995). Upright incubation posture – over an egg resting between (and not on) the feet on a flat or sloping surface (*Uria* spp.) or on the parent's feet (*Aptenodytes* spp.) – almost certainly presents challenges to the incubating bird that could potentially be alleviated by a pyriform egg shape. Indeed, elsewhere we provide clear evidence that the pyriform egg of the Common Guillemot *U. aalge* is much more stable, and hence presumably more easily and safely manipulated by the parent, on a sloping ledge, than is the Razorbill's more elliptical egg (Birkhead *et al.* 2018b). Moreover, the link between incubation posture and egg shape is apparent from the fact that the Razorbill incubates in a horizontal position.

We speculate that an incubating bird might face two challenges that are accentuated by incubating eggs in an upright posture on a flat, often sloping surface. First, the bird must place the egg in such a position that minimizes the chance of it rolling from the incubation site when the adult is not incubating, or during changeovers with their partner. Secondly, when the egg is displaced, the parent must be able to return it to the proper position for efficient incubation. As we have shown elsewhere (Birkhead *et al.* 2018b), eggs that are more pointed and asymmetrical are better able to alleviate those challenges.

Flight efficiency and egg-shape: a contradiction?

Stoddard *et al.* (2017) claim that 'flight efficiency' is an important source of selection on egg shape. In the present study, we have not included any measure of 'flight efficiency' in our statistical models as we feel the HWI is unlikely to be revealing. Moreover, interspecific variation in this feature within the auks and penguins is likely to be very limited given their similar modes of locomotion and the considerable variation in egg shape. Comparison between the HWI of auks and penguins is of limited value because penguins lack conventional wing feathers, and because the alcids fold their wings for underwater flight.

Stoddard *et al.* (2017) variously suggest that 'flight efficiency' is related to 'constrained, muscular streamlined body plans', 'dispersal distance', 'dispersal ability', 'migratory behavior', 'longer and more frequent flight', 'flight strength', 'propensity for sustained flight' and 'flight ability'. In support of this, they present evidence that the hand-wing index is correlated with egg shape such that species with wings that are relatively longer and more pointed have elongated and more-pointed eggs. However, HWI explains only 4% of the total variation in egg shape across the ~1400 species that they studied. Having emphasized the importance of 'flight efficiency', Stoddard *et al.* (2017) also argue that it is not aerodynamic considerations during egg formation that determine egg shape but rather some 'direct or indirect constraint of their aerodynamic body shape'. Nevertheless, there is as yet no evidence that HWI (or other measures of flight ability) is correlated with body shape and reproductive organ size across species; certainly, we would encourage future studies to explore this.

Stoddard *et al.* (2017) did not offer any convincingly plausible mechanism for the statistically significant, but weak, association between HWI and egg shape, and as a result one cannot rule out the possibility of this being a spurious correlation. Our results suggest that, in auks and penguins at least, egg shape is likely to be determined by factors during the incubation period, including the type of breeding site and incubation posture. Assuming that there is a link between avian body conformation and egg shape, as others have suggested (de Lafresnaye 1845, cited in Thompson 1917, Rensch 1947, Warham 1990, Deeming & Mayr 2018), then it is at least feasible that egg shape is driven by anatomical adaptations for locomotion (flight, swimming, walking and diving) but also by the need to incubate efficiently in a variety of situations (a deep cup nest, shallow cup nest, no nest on bare rock, etc.). In our view, and as our results show, it is necessary to consider the physical characteristics of the breeding site and incubation posture, in addition to avian anatomy and locomotion, to identify the selective pressures on avian egg shape.

CONCLUDING REMARKS

As powerful as comparative studies can be, broad-based analyses like that of Stoddard *et al.* (2017) can mask effects that differ from taxon to taxon. The results of our smaller, more fine-scale analyses that include breeding site, suggest that for *Uria* guillemots and *Aptenodyte*s penguins producing pyriform eggs, incubation posture, lack of a nest and associated factors during the incubation phase seem likely to have influenced the evolution of egg shape.

Future research should attempt to determine across a broad range of avian taxa whether a combination of body-plan conformation, locomotion, clutch size and incubation site are the main determinants of egg shape, as we suggest here. The starting point should be to compile a dataset of egg shapes and sizes based on standardized photographs and Preston's (1953, 1968, 1969) model parameters that accurately represent the shapes of all eggs (see Biggins *et al.* 2018).

We thank all the museum curators, and Douglas Russell (NHM Tring) in particular, for allowing us to measure and photograph the eggs in their care. We are grateful to WTSWW (and Lizzie Wilberforce in particular) and Natural Resources Wales for permission to work on Skomer Island and to collect and photograph eggs there. We thank the Skomer wardens Birgitta Buche and Edward Stubbings, and our field assistants for their help. G. Crosin kindly provided information on penguin eggs. We thank Marie Attard, Ben Hatchwell, Duncan Jackson and Nicola Hemmings for comments on the manuscript, and Santiago Claramunt for insights about the problems with HWI as an index of body shape and flight costs. The study was funded by grants from the Leverhulme Trust (to T.R.B.) and the Natural Sciences and Engineering Research Council of Canada (to R.M.). T.R.B. conceived the study; T.R.B. and R.M. wrote the paper; J.E.T. and T.R.B. collected the data; J.E.T. made all the measurements; J.D.B., R.M. and J.E.T. analysed the data. The authors declare no competing interests.

REFERENCES

Andersson, M. 1978. Optimal egg shape in waders. *Ornis Fennica* **55**: 105–109.

Baker, D.E. 2002. A geometric method for determining the shape of bird eggs. *Auk* **119**: 1179–1186.

Barta, Z. & Székely, T. 1997. The optimal shape of avian eggs. *Funct. Ecol.* **11**: 656–662.

Belopol'skii, L.O. 1957. *Ecology of Sea Colony Birds of the Barents Sea*. Jerusalem: Israel Program for Scientific Translations. (Translated from Russian, 1961).

Bengtson, S.-A. 1984. Breeding ecology and extinction of the Great Auk (*Pinguinus impennis*): anecdotal evidence and conjectures. *Auk* **101**: 1–12.

Biggins, J.D., Thompson, J.E. & Birkhead, T.R. 2018. Accurately quantifying the shape of birds' eggs. *Ecol. Evol.* In press. https://doi.org/10.1002/ece3.4412

Birkhead, T.R. 2016. *The Most Perfect Thing: The Inside (and Outside) of a Bird's Egg*. London: Bloomsbury.

Birkhead, T.R., Thompson, J.E. & Biggins, J.D. 2017a. Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemots *U. lomvia*: not a rolling matter? *J. Ornithol.* **158**: 679–685.

Birkhead, T.R., Thompson, J.E., Jackson, D. & Biggins, J.D. 2017b. The point of a Guillemot's egg. *Ibis* **159**: 255–265.

Birkhead, T.R., Thompson, J.E., Biggins, J. D. & Montgomerie, R. 2018a. Supplementary material from: The evolution of egg shape in birds: selection during the incubation period. figshare. Fileset. Available online at https://figshare.com/articles/_/6752882/0 (accessed 24 August 2018).

Birkhead, T.R., Thompson, J.E. & Montgomerie, R. 2018b. The pyriform egg of the common murre *Uria aalge* is more stable on sloping surfaces. *Auk* **135**: 1020–1032, DOI: 10.1642/AUK-18-38.1

Blackburn, T.M. 1991. An interspecific relationship between egg size and clutch size in birds. *Auk* **108**: 973–977.

Coues, E. 1874. *Field Ornithology*. Salem: Naturalists' Agency.

Deeming, D.C. 2018. Effect of composition on shape of bird eggs. *J. Avian Biol.* **49**: 001–007 (Early view).

Deeming, D.C. & Mayr, G. 2018. Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their eggs. *J. Evol. Biol.* **31**: 701–709.

Deeming, D.C. & Ruta, M. 2014. Egg shape changes at the theropod-bird transition, and a morphometric study of amniote eggs. *R. Soc. Open Sci.* **1**: 140311.

Dehnhard, N., Eens, M., Demongin, L., Quillfeldt, P. & Poisbleau, M. 2015. Individual consistency and phenotypic plasticity in rockhopper penguins: female but not male body mass links environmental conditions to reproductive investment. *PLoS One* **10**: e0128776.

Dyke, G.J. & Kaiser, G.W. 2010. Cracking a developmental constraint: egg size and bird evolution. *Rec. Aust. Mus.* **62**: 207–216.

Gaston, A.J. & Jones, I. 1998. *The Auks*. Oxford: Oxford University Press.

Hewitson, W.C. 1831. *British Oology: Being Illustrations of the Eggs of British Birds*. Newcastle upon Tyne: Empson.

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. 2017. *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions. Available at: http://www.hbw.com/ (accessed 11 December 2017).

Huxley, J.S. 1927. On the relation between egg-weight and body-weight in birds. *Zool. J. Linn. Soc.* **36**: 457–466.

Ingold, P. 1980. Anpassungen der Eier und des Brutverhaltens von Trottelummen an das Brüten auf felssimen. *Z. Tierpsychol.* **53**: 341–388.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. 2012. The global diversity of birds in space and time. *Nature* **491**: 444–448.

Juang, J.-Y., Chen, P.-Y., Yang, D.-C., Wu, S.-P., Yen, A. & Hsieh, H.-I. 2017. The avian egg exhibits general allometric invariances in mechanical design. *Sci. Rep.* **7**: 14025.

Ksepka, D.T., Bertelli, S. & Giannini, N.P. 2006. The phylogeny of the living and fossil Sphenisciformes (penguins). *Cladistics* **22**: 412–441.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.

de Lafresnaye, F. 1845. Comparaison des oeufs des oiseaux avec leurs squelettes, comme seul moyen de reconnaitre la cause de leurs différentes forms. *Rev. Zool.* **1845**: 180–187, 239–244.

MacGillivray, W. 1852. *A History of British Birds*. Vol. V: 321. London: William S. Orr and Co.

Mallock, A. 1925. The shapes of birds' eggs. *Nature* **116**: 311–312.

Mao, K.-M., Murakami, A., Iwasawa, A. & Yoshizaki, N. 2007. The asymmetry of avian egg-shape: an adaptation for reproduction on dry land. *J. Anat.* **210**: 741–748.

Nettleship, D.N. & Birkhead, T.R. 1985. *The Atlantic Alcidae*. London: Academic Press.

Preston, F.W. 1953. The shapes of birds' eggs. *Auk* **70**: 160–182.

Preston, F.W. 1968. The shapes of birds' eggs: mathematical aspects. *Auk* **85**: 454–463.

Preston, F.W. 1969. Shapes of birds' eggs: extant North American families. *Auk* **86**: 246–264.

Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M. & Lemmon, A.R. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**: 569–573.

R Core Team 2018. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Rahn, H., Paganelli, C.V. & Ar, A. 1975. Relation of avian egg weight to body weight. *Auk* **92**: 750–765.

Rensch, B. 1947. *Neuere Problem der Abstammungslehre*. Stuttgardt: Ferfinand Enke Verlag.

Ricklefs, R.E. 1983. Avian postnatal development. *Avian Biol.* **7**: 1–83.

Rodewald, P.G. 2017. *The Birds of North America*. New York, NY: Cornell Lab of Ornithology. Available at: https://birdsna.org

Rohwer, F.C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* **105**: 161–176.

Romanoff, A.J. & Romanoff, A.L. 1949. *The Avian Egg*. New York, NY: Wiley.

Schoenwetter, M. 1960–1992. *Handbuch der Oologie*. Berlin: Akamedie Verlag.

Smith, N.A. & Clarke, J.A. 2015. Systematics and evolution of the Pan-Alcidae (Aves, Charadriiformes). *J. Avian Biol.* **46**: 125–140.

Starck, J.M. & Ricklefs, R.E. 1998. Patterns of development: the altricial–precocial spectrum. In Starck, J.M. & Ricklefs, R.E. (eds) *Avian Growth and Development*: 3–30. Oxford: Oxford University Press.

Stein, R.W. & Williams, T.D. 2013. Extreme intraclutch egg-size dimorphism in *Eudyptes* penguins, an evolutionary response to clutch-size maladaptation. *Am. Nat.* **182**: 260–270.

Stoddard, M.C., Young, E.H., Akkaynak, D., Sheard, C., Tobias, J.A. & Mahadevan, L. 2017. Avian egg shape: form, function and evolution. *Science* **356**: 1249–1254.

Thompson, D'.A.W. 1917. *On Growth and Form*. New York, NY: Macmillan.

Thomson, A.L. 1964. *A New Dictionary of Birds*. Edinburgh: Nelson.

Todd, P.H. & Smart, I.H.M. 1984. The shape of birds' eggs. *J. Theor. Biol.* **106**: 239–243.

Tschanz, B., Ingold, P. & Lengacher, H. 1969. Eiform und Bruterfolg bei Trottellummen. *Orn. Beob.* **66**: 25–42.

Walters, M. 1994. *Birds' Eggs*. London: Dorling Kindersley.

Warham, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. London: Academic Press.

Williams, T.D. 1995. *Penguins*. Oxford: Oxford University Press.

Received 24 March 2018;
revision accepted 12 August 2018.
Associate Editor: Francis Daunt.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article. (see also Birkhead et al. 2018a)

Appendix S1. Egg sources and sample sizes.

Appendix S2. Measuring egg shape.

Appendix S3. Statistical analyses.

Appendix S4. Supplementary results.

Figure S1. Outline drawing showing egg-shape indices.

Figure S2. Phylogeny of the alcids and penguins.

Figure S3. Silhouettes of one egg of each species studied, to scale.

Figure S4. Relationship between egg volume and adult body mass (both $\log_{10}$-transformed) for species with different general developmental modes (alcid = precocial, penguin = altricial).

Figure S5. Biplot from PCA with varimax rotation.

Figure S6. Egg-shape morphospace plotted from data in Stoddard *et al.* (2017) with both the entire morphospace (1400 species) and the 20 species they studied that are included in the present study (dashed line) encompassed by convex polygons.

Table S1. Relationships between egg volume, adult body mass, egg-shape indices and taxon (alcid vs. penguin) in 14 alcid and 16 penguin species.

Table S2. Linear models to predict egg-shape indices from general developmental mode (altricial vs. precocial) in 30 species of alcids (*n* = 14) and penguins (*n* = 16), controlling for ($\log_{10}$-transformed) egg volume.

Table S3. Linear models to predict egg-shape indices from clutch size in 14 alcid and 16 penguin species, controlling for egg size and general developmental mode (altricial vs. precocial).

Table S4. Linear models to predict egg-shape indices from incubation site in 14 alcid and 16 penguin species: (a) controlling for egg size, clutch size and general developmental mode (altricial vs. precocial); (b) not controlling for any variables.

Table S5. Loadings of the egg size and shape variables on rotated components (RC1 and RC2) from PCA using the varimax rotation, with data from 14 alcid and 16 penguin species.

Table S6. Top models (ΔAICc < 2) to predict egg shape (RC2) in 14 alcid and 16 penguin species.

Table S7. Best-fitting (see Table S6, model 1) linear model to predict the general egg-shape index (RC2) in relation to incubation site and clutch size in the alcids and penguins.

Table S8. Linear models to predict egg-shape indices using a dataset without three species for which we had measured fewer than five eggs.

Table S9. Linear models to predict general egg shape (RC2) controlling for phylogeny (Fig. S2), based on the (a) full (Table 2 in main text) and (b) best-fitting models (Table S7). Branch lengths in the phylogeny were set to 1.0.

CHAPTER 9:

General Discussion

This thesis presents several published papers that aim to further contribute to the understanding of potential evolutionary drivers and functions of avian egg shape diversity. In particular, these published papers demonstrate: **(i)** the effectiveness of a novel, automated egg shape analysis method using Preston's (1953) modelling approach (Biggins et al. 2018; Chapter 2), in which it is shown (a) that there is greater accuracy in mathematical egg shape modelling methods developed by Preston (1953) compared to several subsequently proposed methods, (b) that, after reviewing numerous previously proposed shape indices, the use of three specific shape indices (i.e. pointedness, elongation and polar asymmetry – as defined in Biggins et al. 2018) provide a solid and intuitive basis for describing all avian egg shapes, and (c) the importance, first, of correctly positioning eggs in photographs for automated 2D-image shape analysis and second, correcting for any lens distortion, to minimise errors of shape quantification; **(ii)** the improbability of the previously proposed 'rolling-in-an-arc' adaptive explanation for the extreme pyriform (pointed) shape of Common Guillemot *Uria aalge* eggs (Birkhead et al. 2017a; Chapter 4); **(iii)** the greater plausibility of alternative novel adaptive hypotheses for the Common Guillemot's pyriform egg, specifically the faecal/debris contamination and stability hypotheses – and the decision that the latter is the more convincing explanation (Birkhead et al. 2017b; Jackson et al. 2018; Birkhead et al. 2018; Chapters 5-7). This latter result indicates the potential importance of incubation site as a selective agent on egg shape variation, and we subsequently show **(iv)** that within the alcids (Alcidae) and penguins (Spheniscidae) egg shape variation is significantly associated with incubation site characteristics, thus further highlighting selection at the incubation stage as a possible major influencer of egg shape diversity (Birkhead et al. 2019; Chapter 8).

Several studies have attempted to examine the potential evolutionary drivers and functions of avian egg shape diversity, although only recently have studies used quantified shape indices to explore these ideas (summarised in Table 1). In particular, Stoddard et al. (2017) made the first attempts to examine the potential global-scale drivers of avian egg shape diversity using phylogenetic comparative analyses of egg shape across more than 1200 bird species. Stoddard et al. (2017) concluded that two main significant predictors of global-scale egg shape diversity patterns were: relative egg size (in relation to adult body mass) and flight ability (using hand-wing index as a proxy for flight ability; Kipp 1959; Lockwood et al. 1998; Claramunt et al. 2012, Pigot & Tobias 2015; Kennedy et al. 2016). Stoddard et al.'s (2017) study is extensive and thought-provoking, but has some serious limitations. These are as follows:

(i) Stoddard et al. (2017) obtained egg shape indices from photographs previously taken by the Museum of Vertebrate Zoology, Berkeley for curatorial purposes (accessible at: *http://arctos.database.museum*). These photographs typically contain multiple eggs together, all of which are in their natural resting positions. Camera lenses often cause optical distortion to photographs and, depending on the specific type of optical distortion, different areas of a given image can be more or less affected. Hence, eggs positioned at different parts of the image are likely to experience varying levels of shape distortion. Automated lens distortion corrective software can address these potential issues (Biggins et al. 2018), however it is unclear whether or not Stoddard et al. (2017) performed such corrections on the images in their study. Furthermore, photographing eggs in their natural resting positions can also distort egg shape and result in erroneous measurements of shape indices – particularly for eggs with greater asymmetry and elongation (see Fig. SF3 in Biggins et al. 2018 Supplementary Material) – to those obtained if an egg was correctly positioned with its maximum length axis parallel to the camera lens (Biggins et al. 2018).

(ii) Stoddard et al. (2017) utilised modelling methods developed by Baker (2002) to obtain their shape indices but, as shown in Chapter 2 (Biggins et al. 2018), these methods (and others e.g. Carter 1968; Carter & Morley Jones 1970) generate greater errors than those developed by Preston (1953). Specifically, Baker's (2002) methods struggle to accurately model and quantify shape of more extreme egg types, such as the pyriform eggs of Common Guillemots (see Biggins et al. 2018). As a consequence of these poor Baker (2002) model fits, Stoddard et al. (2017) excluded species with extreme egg forms from their analyses. To better understand the global-scale drivers of avian egg shape diversity, it is obviously essential that *all* egg shape variations are included in any analyses. The availability of 2D-image shape analysis processing software (Biggins et al. 2018) that accurately quantifies the shape of even extreme egg forms, means that the potential now exists to re-examine or check Stoddard et al.'s (2017) conclusions.

Table 1| Summary of predictors and functions of egg shape diversity, at different taxonomic scales, presented within the current scientific literature. Only studies that have explicitly tested these potential predictors and functions against quantified shape indices of actual eggs are included.

Taxonomic Grouping	Predictors/Functions	Reference
All birds	Flight Ability, Relative Egg Size, Temperature	Stoddard et al. 2017
All birds	Pelvis Shape	Shatkovska et al. 2018
All birds	Absolute Egg Mass, Proportion of Yolk, Proportion of Shell, Relative Egg Mass	Deeming 2018
Passeriformes	Flight Ability, Relative Egg Size	Stoddard et al. 2017
Passeriformes (Australian Passerines)	Nest Site (Cavity vs. Cup-shaped), Climatic Conditions (Vapour Pressure Deficit and Leaf Area Index)	Duursma et al. 2018
Charadriiformes	Relative Egg Size, Developmental Mode, Nest Site (Cavity vs. Non-Cavity Ground)	Stoddard et al. 2017
Seabirds (polyphyletic grouping)	Relative Egg Size	Stoddard et al. 2017
Alcidae and Spheniscidae (Auks and Penguins)	Egg Volume, Clutch Size, Breeding Site	Birkhead et al. 2019
Australian Cuckoos (Brush-tailed cuckoo *Cacomantis variolosus* and Pallid cuckoo *Cuculus pallidus*)	Brood parasite egg shape mimicry	Attard et al. 2017
Common Guillemots *Uria aalge*	Stability	Birkhead et al. 2018
Common Guillemots *Uria aalge*	Egg displacement and rolling-in-an-arc behaviour	Hays & Hauber 2018

Nevertheless, Stoddard et al.'s (2017) results suggest that differing anatomical constraints across species act as the key driver of avian egg shape diversity. Specifically, Stoddard et al. (2017) propose that morphological adaptations for flight might have subsequently created anatomical constraints and selection on egg shape. Considering egg size might, at the very least, positively correlate with initial post-hatching chick survival (see Williams 1994; Christians 2002), Stoddard et al. (2017) suggest when egg width is restricted by the anatomical constraints of an aerodynamic body plan, that selection to maximise egg size during formation might occur through the increase of asymmetry and/or ellipticity (i.e. the ratio of egg length to the equatorial diameter – this a similar, but not identical, measurement to elongation *sensu* Biggins et al. 2018).

Previous studies have suggested correlations between egg and pelvis shape and size (Rensch 1947; Warham 1990; Anten-Houston et al. 2018; Deeming 2018; Shatkovska et al. 2018). Considering that pelvis shape variation appears to correlate with birds' locomotive style (Anten-Houston et al. 2018), it is possible that Stoddard et al.'s (2017) finding that flight ability drives egg shape variation might reflect associated changes to pelvis shape and size, which then directly results in changes to egg shape. However, further work is needed to establish the possible correlations between hand-wing index measures and other anatomical features that might establish the direct physiological mechanisms for changes to egg shape (Birkhead et al. 2019; Stoddard et al. 2019).

The extent to which the pelvis might act as an important driver of avian egg shape variation is unclear and perhaps debatable. First, pubic bone fusion, as seen in Jurassic and Cretaceous birds (Dyke & Kaiser 2010; Deeming & Mayr 2018), is absent in modern birds and so constraints on traits such as egg width are somewhat reduced. Second, whilst there may be apparent evidence for the degree of elongation being determined by pelvis shape (Shatkovska et al. 2018), albeit weakly, it is unclear how such anatomical constraints might influence asymmetry. Indeed, Shatkovska et al. (2018) found little association with pelvis shape and the degree of egg asymmetry. Furthermore, any correlations between pelvis and egg shape phenotypes appear to be evident only when species with extreme pelvis morphologies are compared (Shatkovska et al. 2018). Although only very small interspecific differences in pelvis shape exist, there is considerable egg shape diversity between species, suggesting other factors might be driving egg shape diversity (Shatkovska et al. 2018).

It is possible that egg shape is determined (or influenced) by other anatomical constraints not yet extensively investigated, such as the anatomical properties of the oviduct itself and/or the pressure exerted by visceral organs, attached musculature and ligaments on the oviduct (Smart 1991; Deeming 2018). However, in order to examine these potential alternative anatomical constraints, future studies need to both better ascertain the precise mechanisms of egg shape formation (Birkhead 2016; Deeming 2018) and collect the necessary data to establish whether relationships between these anatomical features and egg shape exist. However, given that birds have the ability to lay double-yolked eggs of larger sizes to those typically laid (see Romanoff & Romanoff 1949; Birkhead 2016; Birkhead et al. 2017a), this suggest somewhat flexible and weakened anatomical constraints to egg formation and, consequently, egg shape.

Although Stoddard et al. (2017) reported only relative egg size and flight ability as significant predictors of avian egg shape, in their revised Supplementary Materials they also detected a possible effect of temperature (see Stoddard et al. 2017 Table S2-B in their revised Supplementary Materials). That temperature may be a significant predictor may have an important consequence on the overall interpretation of Stoddard et al.'s (2017) results since this could imply a role of the incubation environment, and possibly other factors related to incubation, on egg shape selection.

Given that the duration of incubation is considerably longer (Rahn & Ar 1974; Ricklefs & Starck 1998; Deeming 2002) than the brief period of egg formation (< 24 hours), as well as the vast differences in incubation environments and behaviours exhibited by birds (Deeming 2002; del Hoyo et al. 2020), it is reasonable to expect that various egg traits, including egg shape, might be optimised to certain incubating conditions for which an egg is exposed to (Hoyt 1976; Deeming 2002). Indeed, previous studies have already implicated that egg shape diversification could be adaptations associated with the incubation stage by demonstrating associations with incubation efficiency (Andersson 1978), clutch size (Barta & Székely 1997; but see Hutchinson 2000; Stoddard et al. 2017), hatchability (Mao et al. 2007), eggshell strength (Bain 1991), and embryo respiration (Smart 1991; Mao et al. 2007). Although evidence for temperature acting as a significant predictor of egg shape adds further support to adaptive selection at the incubation stage, it is somewhat surprising that Stoddard et al. (2017) found no other factors relating to climate and nest characteristics to be significant drivers of overall global-scale avian egg shape diversity patterns; especially considering the prolonged time period for adaptive selective forces to act upon egg traits during incubation.

Rather than direct selection on egg shape phenotypes, optimised incubation efficiency and success might instead have been achieved through selection on parental incubating behaviours and/or other egg traits across birds. However, such selection might still secondarily select for certain egg shape traits (e.g. Duursma et al. 2018). If in fact selection is exerted on other traits relating to incubation rather than directly egg shape *per se*, this may explain the lack of significant predictors for global-scale egg shape patterns relating to incubation that Stoddard et al. (2017) reported. It is also possible that, at least when looking at broad-taxonomic level patterns of egg shape diversity, potentially important incubation stage selective forces on egg shape might be masked (Hall 2011), and this could be further exacerbated in Stoddard et al.'s (2017) study due to the exclusion of species with extreme egg forms from their analyses. The potential for different drivers of avian egg shape diversity patterns at different taxonomic scales has been acknowledged by Stoddard et al. (2017, 2019), and accordingly they make attempts to examine patterns at smaller taxonomic levels (Stoddard et al. 2017). However, in their revised analyses, although they find evidence for nest characteristics driving egg shape in Charadriiformes, no significant evidence that factors relating to the incubating environment drive egg shape variations was found for certain monophyletic (Passeriformes) and polyphyletic (seabirds) groupings (see Supplementary Materials in Stoddard et al. 2017). Stoddard et al.'s (2017) lack of significant correlation between temperature and egg shape in Passeriformes seems to contradict the findings of Duursma et al. (2018), who found that climatic conditions explain some of the variation in egg shape among Australian passerines.

By examining taxa that exhibit extreme and/or diverse egg shape, incubating environments and/or behaviours, researchers might gain clearer insights into the selection pressures on egg shape during incubation (Barnett and Lewis 1994). Both the alcids (Alcidae) and penguins (Spheniscidae) exhibit considerable interspecific variation in egg shape (Stoddard et al. 2017; Birkhead et al. 2019), but also extreme and diverse incubation environments and behaviours (Nettleship & Birkhead 1985; Williams 1995; Gaston & Jones 1998; del Hoyo et al. 2020). Hence, these specific taxa are the focus for the published research presented in Chapters 3-8 of this thesis.

Common Guillemots have both an extreme pyriform egg shape (Tschanz et al. 1969; Birkhead 1993; Birkhead et al. 2017a, b; Stoddard et al. 2017) and a unique breeding environment (Tschanz et al. 1969; Ingold 1980), making them an ideal species to examine potential adaptive selection mechanisms on egg shape. The popular explanation for the Common Guillemot's pyriform egg shape has been the 'rolling-in-an-arc' hypothesis (Belopol'skii 1961) although the evidence for this has been mixed and limited (Tschanz et al. 1969; Ingold 1980). In Chapter 4 (Birkhead et al. 2017a), we raise further doubt about this hypothesis by finding no evidence for the shape-mass hypothesis proposed by Ingold (1980), to explain the anomaly of Brünnich's Guillemots *Uria lomvia* having less pointed eggs than Common Guillemots despite breeding on narrower ledges. Birkhead et al. (2017a) demonstrates that both *Uria* species have eggs of similar mass but Brünnich's Guillemot eggs still have significantly lower pointedness (asymmetry), which is inconsistent with Ingold's (1980) hypothesis. Recently, Hays & Hauber (2018) re-examined the rolling-in-an-arc hypothesis and suggest that increased asymmetry results in greater displacement of eggs, which would potentially address the Brünnich's Guillemot observational anomaly noted by Ingold (1980). However, Hays & Hauber's (2018) study used model eggs, rather than real eggs, that we know do not behave in the same way (T.R. Birkhead and J.E.Thompson *pers. obs.*; also see Tschanz et al. 1969; Ingold 1980) and thus it is unclear whether their findings are biologically meaningful.

Work presented in Chapters 5 and 7 (Birkhead et al. 2017b, 2018) instead proposes several novel alternative hypotheses that might provide more plausible adaptive explanations, to that of the rolling-in-an-arc hypothesis, for the Common Guillemot's pyriform egg shape (Chapters 5 and 7, Birkhead et al. 2017b, 2018): (i) the prevention of mechanical damage hypothesis; (ii) the faecal-debris contamination hypothesis, and (iii) the stability hypothesis. Whilst we have not yet been able to adequately examine the plausibility of the prevention of mechanical damage hypothesis, the faecal-debris contamination hypothesis has some evidence that provides some support for its plausibility, such as demonstrated greater exposure to contamination in Common Guillemots than Razorbills and the reduced contamination risk of blunt regions of guillemot eggs that are the most porous regions (Chapter 5 Birkhead et al. 2017b). Additionally, contamination of eggshell fragments does result in reduced porosity for gaseous exchange (Chapter 6, Jackson et al. 2018), and so selection might act to mitigate this negative consequence. Fully testing the faecal-debris contamination hypothesis would likely require manipulation and cross-fostering experiments of Common Guillemot and Razorbill eggs, however, this would be ethically and morally challenging. Currently, the stability hypothesis has the strongest experimental support (Chapter 7, Birkhead et al. 2018).

After establishing adaptive functions of egg shape at a species level for Common Guillemots, Chapter 8 (Birkhead et al. 2019) examines patterns of egg shape diversity at the broader taxonomic groupings of alcids and penguins, and demonstrates that incubation environments and behaviours explain over 60% of the variation in egg shape in these two taxa. In particular, Birkhead et al. (2019) suggests that breeding site and incubation posture might influence the parents' abilities to manipulate their eggs, which results in differing selection pressures on egg shape.

Other studies have also considered the potential of other incubation characteristics, such as brood patch shape and number (Thompson 1942; Lack 1968; Drent 1975), to drive selection for varying egg shapes. Given the relationship between incubation environments and egg shape in auks and penguins (Birkhead et al. 2019), future studies should explore these potential selective drivers of egg shape variation in other avian taxa. In particular, examining megapodes (Megapodiidae), where underground nests instead provide a heat source to incubating eggs instead of contact incubation behaviours (Booth & Jones 2002), might provide other interesting insights into possible relationships between incubation characteristics and egg shape. Many megapode species lay very elongate eggs that are remarkably similar in shape to those of reptiles (Preston 1969; Iverson & Ewert 1991), which, like megapodes, generally do not exhibit contact incubation behaviour (Deeming et al. 2006). Megapode egg shape appears to be, in part, driven by their large relative size to the adult body size (Jones et al. 1995). However, megapode chicks do not use an egg-tooth at hatching and instead hatch by using their feet and shoulders to break out of the egg (Frith 1959, 1962; Jones et al. 1995; Seymour 1984, 1991; Vleck et al. 1984; Göth 2001; Booth & Jones 2002) and there are strong selective pressures for chicks to hatch out quickly (Seymour 1984; Jones et al. 1995). Hence, considering these unique hatching behaviours and pressures, it is possible that the distinct shape of megapode eggs, alongside their considerably thin eggshell thickness (Seymour & Ackerman 1980; Booth 1988; Jones et al. 1995), may assist with chick hatching. Specifically, pronounced elongation and reduced pointedness/asymmetry of egg shape might provide the chick with an internal space that makes the use of legs and shoulders for hatching more efficient, thus enabling the necessary quick hatching.

Future studies should continue to explore the ways both anatomical constraints and incubation factors drive egg shape patterns (Birkhead et al. 2019; Stoddard et al. 2019). Studies should also adopt a consistent approach to quantifying egg shape to allow greater clarity and easier comparisons between different studies. Another priority is to ascertain the precise mechanisms of egg shape formation and any anatomical constraints on it. Additionally, future studies should continue targeting taxa that demonstrate extreme egg forms and unique incubation characteristics to better establish the various selective pressures during the incubation period that may also drive egg shape variation. Finally, many studies to date have used museum egg collections to explore avian egg shape (e.g. Stoddard et al. 2017; Deeming 2018; Duursma et al. 2018; Birkhead et al. 2019), and are likely to do so in future. An important assumption when using museum collections is that these accurately reflect the typical variation that occurs in natural populations (but see Väisänen 1969; Koenig 1980; Mallory et al. 2004; Birkhead 2016; Birkhead & Montgomerie 2018; Cooper et al. 2019). To assess whether or not this is the case, future studies should prioritise examining the extent of collection biases through comparisons between the observed variations in egg shape phenotypes within collections and in natural populations, and modelling the effects of any violations of the assumption. Indeed, this is something that my work colleague and I have begun to examine (Thompson & Birkhead *in prep.*, presented in Appendix 1).

By adopting these suggested research avenues, it is my hope that this will enable future studies to provide greater clarity of the drivers and functions of avian egg shape diversity and the likely complex interactions between them.

References in Chapter 9:

Andersson, M. (1978). Optimal egg shape in waders. *Ornis Fennica*, **55**, 105-109.

Anten-Houston, M. V., Ruta, M. and Deeming, D. C. (2017). Effects of phylongeny and locomotor style on the allometry of body mass and pelvic dimensions in birds. *Journal of Anatomy*, **231**, 342-358.

Attard, M. R. G., Medina, I., Langmore, N. E., and Sherratt, E. (2017). Egg shape mimicry in parasitic cuckoos. *Journal of Evolutionary Biology*, **30**, 2079-2084.

Bain, M. M. (1991). A reinterpretation of eggshell strength. In: *Egg and Eggshell Quality.* (ed. Solomon, S. E.). Wolfe Publishing Limited: London. pp. 131-145.

Baker, D. E. (2002). A Geometric Method for Determining Shape of Bird Eggs. *The Auk*, **119**, 1179-1186.

Barta, Z. and Székely, T. (1997). The optimal shape of avian eggs. *Functional Ecology*, **11**, 656-662.

Belopol'skii, L. O. (1961). *Ecology of Sea Colony Birds of the Barents Sea.* (translated from original 1957 publication by Ettinger R. and Salzmann C.). Israel Program for Scientific Translations: Jerusalem.

Biggins, J. D., Thompson, J. E. and Birkhead, T. R. (2018). Accurately quantifying the shape of birds' eggs. *Ecology and Evolution*, **8**, 9728-9738.

Birkhead, T. R. (1993). *Great Auk Islands: A Field Biologist in the Arctic.* Poyser: London.

Birkhead, T. R. (2016). *The Most Perfect Thing: The Inside (and Outside) of a Bird's Egg.* Bloomsbury: London.

Birkhead, T. R. and Montgomerie, R. (2018). Rare red eggs of the Common Guillemot (*Uria aalge*): birds, biology and people at Bempton, Yorkshire, in the early 1900s. *Archives of Natural History*, **45**, 69-79.

Birkhead, T. R., Thompson, J. E. and Biggins, J. D. (2017a). Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: not a rolling matter? *Journal of Ornithology*, **158**, 679-685.

Birkhead, T. R., Thompson, J. E., Jackson, D. and Biggins, J. D. (2017b). The point of a Guillemot's egg. *Ibis*, **159**, 255-265.

Birkhead, T. R., Thompson, J. E. and Montgomerie, R. (2018). The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *The Auk*, **135**, 1020-1032.

Birkhead, T. R., Thompson, J. E., Biggins, J. D. and Montgomerie, R. (2019). The evolution of egg shape in birds: selection during the incubation period. *Ibis*, **161**, 605-618.

Booth, D. T. (1988). Shell thickness in megapode eggs. *Megapode Newsletter*, **2**, 13.

Booth, D. T. and Jones, D. N. (2002). Underground nesting in the megapodes. In: *Avian Incubation: Behaviour, Environment and Evolution* (ed. Deeming, D. C.). Oxford University Press: Oxford. pp. 192-206.

Carter, T. C. (1968). The hen's egg: A mathematical model with three parameters. *British Poultry Science*, **9**, 165-171.

Carter, T. C. and Morley Jones, R. (1970). The hen's egg: Shell shape and size parameters and their interrelations. *British Poultry Science*, **11**, 179-188.

Christians, J. K. (2002). Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews*, **77**, 1-26.

Claramunt, S., Derryberry, E. P., Remsen, J. V. and Brumfield, R. T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1567-1574.

Cooper, N., Bond, A. L., Davis, J. L., Miguez, R. P., Tomsett, L. and Helgen, K. M. (2019). Sex biases in bird and mammal natural history collections. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 20192025.

Deeming, D. C., ed. (2002). Avian Incubation: Behaviour, Environment and Evolution. Oxford University Press: Oxford.

Deeming, D. C. (2018). Effect of composition on shape of bird eggs. *Journal of Avian Biology*, **49**, e01528.

Deeming, D. C., Birchard, G. F., Crafer, R. and Eady, P. E. (2006). Egg mass and incubation period allometry in birds and reptiles: effects of phylogeny. *Journal of Zoology*, **270**, 209-218.

Deeming, D. C. and Mayr, G. (2018). Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their eggs. *Journal of Evolutionary Biology*, **31**, 701-709.

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. and de Juana, E., eds. (2020). *Handbook of the Birds of the World Alive*. Lynx Edicions: Barcelona. Available at: http://www.hbw.com/ (accessed 15 January 2020).

Drent, R. (1975). Incubation. In: *Avian Biology, Volume 5.* (eds. Farner, S., King, J. R. and Parkes, K. C.). Academic Press: New York. pp. 333-420.

Duursma, D. E., Gallagher, R. V., Price, J. J. and Griffith, S. C. (2018). Variation in avian egg shape and nest structure is explained by climatic conditions. *Scientific Reports*, **8**, 4141.

Dyke, G. J. and Kaiser, G. W. (2010). Cracking a Developmental Constraint: Egg Size and Bird Evolution. *Records of the Australian Museum*, **62**, 207-216.

Frith, H. J. (1959). Breeding in the malleefowl, *Leiopa ocellate* Gould (Megapodiidae). *CSIRO Wildlife Research*, **4**, 31-60.

Frith, H. J. (1962). *The Mallee Fowl.* Angus and Robertson: Sydney.

Gaston, A. J. and Jones, I. L. (1998). *The Auks.* Oxford University Press: Oxford.

Göth, A. (2001). *Survival, habitat selectivity and behavioural development of Australian brush turkey Alectura lathami chicks*. PhD Thesis, Griffith University, Brisbane, Australia.

Hall, B. K. (2011). *Evolution: Principles and Processes.* Jones and Bartlett Learning: Burlington.

Hays, I. R. and Hauber, M. E. (2018). How the egg rolls: a morphological analysis of avian egg shape in the context of displacement dynamics. *Journal of Experimental Biology*, **221**, jeb178988.

Hoyt, D. F. (1976). The Effect of Shape on the Surface-Volume Relationships of Birds' Eggs. *The Condor*, **78**, 343-349.

Hutchinson, J. M. C. (2000). Three into two doesn't go: two-dimensional models of bird eggs, snail shells and plant roots. *Biological Journal of the Linnean Society*, **70**, 161-187.

Ingold, P. (1980). Anpassungen der Eier und des Brutverhaltens von Trottellummen (*Uria aalge aalge* Pont.) an das Brüten auf Felssimsen. *Zeitschrift für Tierpsychologie*, **53**, 341-388.

Iverson, J. B. and Ewert, M. A. (1991). Physical characteristics of reptilian eggs and a comparison with avian eggs. In: *Egg Incubation: Its effects on embryonic development in birds and reptiles.* (eds. Deeming, D. C. and Ferguson, M. W. J.). Cambridge University Press: Cambridge. pp. 87-100.

Jackson, D., Thompson, J. E., Hemmings, N. and Birkhead, T. R. (2018). Common guillemot (*Uria aalge*) eggs are not self-cleaning. *Journal of Experimental Biology*, **221**, jeb188466.

Jones, D. N., Dekker, R. W. R. J. and Roselaar, C. S. (1995). *The Megapodes.* Oxford University Press: Oxford.

Kennedy, J. D., Borregaard, M. K., Jønsson, K. A., Marki, P. Z., Fjeldså, J. and Rahbek, C. (2016). The influence of wing morphology upon the dispersal, geographical distributions and diversification of the Corvides (Aves; Passeriformes). *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20161922.

Kipp, F. A. (1959). Der Handflügel-Index als flugbiologisches Maß. *Die Vogelwarte*, **20**, 77-86.

Koenig, W. D. (1980). The Determination of Runt Eggs in Birds. *The Wilson Bulletin*, **92**, 103-107.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds.* Methuen: London.

Lockwood, R., Swaddle, J. P. and Rayner, J. M. V. (1998). Avian Wingtip Shape Reconsidered: Wingtip Shape Indices and Morphological Adaptations to Migration. *Journal of Avian Biology*, **29**, 273-292.

Mallory, M. L., Kiff, L., Clark, R. G., Bowman, T., Blums, P., Mednis, A. and Alisauskas, R. T. (2004). The occurrence of runt eggs in waterfowl clutches. *Journal of Field Ornithology*, **75**, 209-217.

Mao, K-M., Murakami, A., Iwasawa, A. and Yoshizaki, N. (2007). The asymmetry of avian egg-shape: an adaptation for reproduction on dry land. *Journal of Anatomy*, **210**, 741-748.

Nettleship, D. N. and Birkhead, T. R., eds. (1985). *The Atlantic Alcidae.* Academic Press: London.

Pigot, A. and Tobias, J. A. (2015). Dispersal and the transition to sympatry in vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20141929.

Preston, F. W. (1953). The Shapes of Birds' Eggs. *The Auk*, **70**, 160-182.

Preston, F. W. (1969). Shapes of Birds' Eggs: Extant North American Families. *The Auk*, **86**, 246-264.

Rahn, H. and Ar, A. (1974). The Avian Egg: Incubation Time and Water Loss. *The Condor*, **76**, 147-152.

Rensch, B. (1947). *Neuere Probleme der Abstammungslehre.* Ferdinand Enke: Stuttgart.

Ricklefs, R. E. and Starck, J. M. (1998). Embryonic Growth and Development. In: *Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum.* (eds. Starck, J. M. and Ricklefs, R. E.). Oxford University Press: Oxford. pp. 31-58.

Romanoff, A. L. and Romanoff, A. J. (1949). *The Avian Egg.* John Wiley & Sons, Inc.: New York.

Seymour, R. S. (1984). Patterns of lung aeration in the perinatal period of domestic fowl and brush turkey. In: *Respiration and Metabolism of Embryonic Vertebrates.* (ed. Seymour, R. S.). Junk Publishers: Dordrecht. pp. 319-332.

Seymour, R. S. (1991). The Brush Turkey. *Scientific American*, **265**, 68-74.

Seymour, R. S. and Ackerman, R. A. (1980). Adaptations to Underground Nesting in Birds and Reptiles. *American Zoologist*, **20**, 437-447.

Shatkovska, O. V., Ghazali, M., Mytiai, I. S. and Druz, N. (2018). Size and shape correlation of birds' pelvis and egg: Impact of developmental mode, habitat, and phylogeny. *Journal of Morphology*, **279**, 1590-1602.

Smart, I. H. M. (1991). Egg shape in birds. In: In: *Egg Incubation: Its effects on embryonic development in birds and reptiles.* (eds. Deeming, D. C. and Ferguson, M. W. J.). Cambridge University Press: Cambridge. pp. 101-116.

Stoddard, M. C., Sheard, C., Akkaynak, D., Yong, E. H., Mahadevan, L. and Tobias, J. A. (2019). Evolution of avian egg shape: underlying mechanisms and the importance of taxonomic scale. *Ibis*, **161**, 922-925.

Stoddard, M. C., Yong, E. H., Akkaynak, D., Sheard, C., Tobias, J. A. and Mahadevan, L. (2017). Avian egg shape: Form, function and evolution. *Science*, **356**, 1249-1254.

Thompson, D'A. W. (1942). *On Growth and Form.* Cambridge University Press: Cambridge.

Tschanz, B., Ingold, P. and Lengacher, H. (1969). Eiform und Bruterfolg bei Trottellummen (*Uria aalge*). *Ornithologische Beobachter*, **66**, 25-42.

Väisänen, R. A. (1969). Evolution of the ringed plover (*Charadrius hiaticula* L.) during the last hundred years in Europe. A new computer method based on egg dimensions. *Annales Academiae Scientiarum Fennicae Series A: IV, Biologica*, **149**, 1–90.

Vleck, D., Vleck, C. M. and Seymour, R. S. (1984). Energetics of embryonic development in the megapode birds, Mallee Fowl *Leipoa ocellate* and Brush Turkey *Alectura lathami*. *Physiological Zoology*, **57**, 444-456.

Warham, J. (1990). *The Petrels: Their Ecology and Breeding Systems.* Academic Press: London.

Williams, T. D. (1994). Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews*, **68**, 35-59.

Williams, T. D. (1995). *The Penguins.* Oxford University Press: Oxford.

APPENDIX 1:

Avian egg collections: museum collection bias driven by shape and size

Avian egg collections: museum collection bias driven by shape and size

Thompson, J. E. and Birkhead, T. R. (in prep.)

Paper context and thesis author's contributions: Recent studies exploring avian egg shape have often used museum egg collections to investigate their question(s) of interest, and this is likely to continue in future. When using museum egg collections, it is assumed that they accurately reflect natural variations in egg shape traits for a given species and are therefore appropriate to sample. However, previous researchers have acknowledged the potential for collection bias to have an impact on trait representation within various natural history museum collections, and there is yet to be any studies that have examined the extent of collection bias based on shape and size traits within museum egg collections. Here, the aim of this study was to compare the observed variations in egg shape indices between museum collections and eggs recently collected in the field of three bird species and to begin to assess whether or not collection bias is evident in any of the museum egg collections.

My contribution to this published article comprised of conceiving and developing the study. I measured and photographed eggs within the field (under licence) and in museum collections. I performed all the automated shape analysis script runs and collated the data. All statistical analyses were done by myself. I wrote the original draft manuscript and assisted with the improvements of subsequent re-drafts.

Co-authors' contributions: T.R. Birkhead helped conceive the study. T.R. Birkhead assisted with the measuring of eggs and contributed improvements to the re-drafts of the manuscript.

Avian egg collections: museum collection bias driven by shape and size

Jamie E. Thompson[1*] and Tim R. Birkhead[1]

[1] Department of Animal & Plant Sciences, The University of Sheffield, Alfred Denny Building, Western Bank. S10 2TN.

[*] Corresponding Author: jamie.thompson@sheffield.ac.uk

Abstract

Avian eggs exhibit considerable intra- and interspecific variation in shape, size and colour. Considerable efforts have been made to better understand the evolutionary drivers behind such variation, often using museum egg collections. Usually it is assumed that museum collections accurately represent the variation seen in natural populations, but this may not be the case if there is collection bias. Collection bias may lead to the over-representation of certain egg traits in collections, due to the aesthetic (or other) preferences of collectors. Using recently developed methods for measuring egg shape and size, this study examines evidence for collection bias in museum egg collections by comparing three shape indices (pointedness/asymmetry, elongation and polar asymmetry) and egg volume between museum collections and recently sampled eggs in the field for three different bird species: Common Guillemot *Uria aalge*, Razorbill *Alca torda*, and Northern Fulmar *Fulmarus glacialis*. We found no evidence of collection bias in museum collections of Razorbill and Northern Fulmar eggs, but some evidence for a bias in Common Guillemot eggs. Since the guillemot's egg differs from most bird eggs in being pyriform, we suggest that collection bias by historic egg collectors may be more prevalent in species with extreme egg traits. Researchers using egg collections to examine questions relating to egg shape should consider how to minimise the effect of these potential biases.

Keywords: Avian egg shape; Museum egg collections; Pointedness; Elongation; Polar Asymmetry; Guillemots

Introduction

Across and within bird species there is considerable variation in egg shape, colour and maculation (shape: Hewitson 1831; Thompson 1917; Thomson 1964; Stoddard et al. 2017, and colour and maculation: Wallace 1889; Gaston & Nettleship 1981; Kilner 2006; Cassey et al. 2010a; Cherry & Gosler 2010; Stevens 2011, also see Birkhead 2016). Variation in both intra- and interspecific egg traits has long intrigued researchers (e.g. Hewitson 1831; Wallace 1889; Newton 1896; Swynnerton 1916; Thompson 1917; Schönwetter 1960-1992), but the drivers of egg trait variation remain poorly understood (Underwood & Sealy 2002; Cassey et al. 2010a; Deeming & Ruta 2014; Birkhead 2016; Stoddard *et al.* 2017; Birkhead et al. 2019; Stoddard et al. 2019b). Recent studies have started to fill this gap in our understanding by examining patterns of egg trait diversity at different taxonomic scales (e.g. shape: Birkhead et al. 2017a, 2017b, 2018, 2019; Stoddard et al. 2017; Deeming 2018; Duursma et al. 2018; Shatkovska et al. 2018, and colour and patterning: Spottiswoode & Stevens 2011; Hauber et al. 2019**;** Stoddard et al. 2019a).

Although some studies of egg trait variation use newly collected samples (e.g. Spottiswoode & Stevens 2011; Birkhead et al. 2018; Stoddard et al. 2019a), most use museum collections (e.g. Stoddard & Stevens 2010; Attard et al. 2017; Birkhead et al. 2017a, 2019; Stoddard et al. 2017; Deeming 2018; Duursma et al. 2018). Museum collections are a valuable resource for researchers and have contributed to an improved understanding of various aspects of bird biology, including the effects of chemical pollutants on eggshell thickness (Ratcliffe 1967; Hickey & Anderson 1968; Newton et al. 1982; Green 1998); genome-wide evolutionary processes underpinning temporal avian diversity changes (Grealy et al. 2019); and brood parasite-host coevolution (e.g. Stoddard & Stevens 2010; Stoddard et al. 2014; Attard et al. 2017). Recent studies have also used museum collections to explore the evolutionary drivers of variation in egg shape variation (e.g. Birkhead et al. 2017b, 2019; Stoddard et al. 2017; Deeming 2018; Duursma et al. 2018).

Museum egg collections clearly have a valuable role in scientific research, but some studies have recommended they be used with caution due to the potential effects of collection bias (e.g. Lack 1946; Väisänen 1969; Koenig 1980; McNair 1987; Mallory et al. 2004; Starling et al. 2006; Birkhead & Montgomerie 2018), something that has also been noted in other types of natural history collections (Cooper et al. 2019). Although some eggs in museum collections were collected in a random (or at least haphazard) manner, such as those sampled during scientific expeditions, many were collected by individual collectors either for a hobby or to sell. These people may have been motivated to assemble a particular series of eggs for aesthetics, oddity and rarity that may have made certain eggs more attractive (Väisänen 1969; Koenig 1980; Mallory et al. 2004; Birkhead 2016; Birkhead & Montgomerie 2018). Accordingly, previous studies have highlighted that historic collectors might have preferentially searched for rare egg colours, such as erythristic (red) eggs in Common Guillemots *Uria aalge* (Birkhead & Montgomerie 2018) and corvids (Trobe & Whitaker 2014), or eggs of unusual shape and/or sizes (Väisänen 1969; Koenig 1980; Mallory et al. 2004; Birkhead et al. 2017a).

Museum egg collections are typically accompanied with data cards, so it is sometimes possible to use this information to remove samples with obvious abnormalities, mistaken/mismatched data information, and/or clearly biased collection motives (McNair 1987). However, data cards are not always available and, even if they are, do not always contain the information necessary for sample exclusion. In the absence of such information, assessing whether a collection is representative of a wild population can be difficult.

Previous researchers have noted that both the rarity of a species, as well as the accessibility of its breeding sites, may influence the potential for collection bias (Väisänen 1969). It is also possible that collection bias might be dependent on the extent of natural variation in egg traits in a given population/species. If a population exhibits low variation in a particular egg trait (so that eggs are relatively uniform), this would be expected to reduce the potential risk of collection bias. In contrast, a population with high variation in a particular egg trait might be more at risk to collection bias, because more extreme trait values may be more attractive to collectors (e.g. Birkhead 2016; Birkhead & Montgomerie 2018). When considerable variation occurs in a given egg trait, egg collectors have typically strived to obtain examples of eggs exhibiting as many different varieties of that trait as possible, rather than selecting a representative set of eggs randomly (Väisänen 1969). Such biases may lead to a skewed representation of natural variation in many egg traits within museum egg collections.

The aim of this study was to explore possible collection biases in egg shape and size. Although some studies have explored potential sources of bias in egg colour within museum egg collections and subsequently how to appropriately sample museum eggs for such traits (e.g. Cassey et al. 2010b;

Moreno et al. 2011), there have been no studies that have examined collection bias with respect to egg shape and size. We therefore looked to examine the extent of such collection bias by comparing shape and size traits of eggs from museum collections to those recently collected from the field (henceforth referred to as the 'field collection') for three bird species whose eggs were commonly collected and that demonstrate differing extremities of egg shape: Common Guillemot, Razorbill *Alca torda* and Northern Fulmar *Fulmarus glacialis*.

Methods

Field collection egg sampling

To sample eggs for our field collection, we selected breeding sites based on how safely accessible they were and then all available eggs from those selected sites were sampled. Whilst not truly random, the sampling of all eggs available on a given breeding ledge should have removed individual conscious or subconscious sampling biases.

Comparing eggs from the field and museum collections

Since egg size can vary geographically (e.g. Harris and Birkhead 1985; Hendricks 1991), we compared field collections with museum collections of eggs from colonies as geographically close as possible. Ideally, we would have also compared eggs collected in the same breeding year (since egg size can change between breeding seasons; Mänd & Tilgar 2004; Tryjanowski et al. 2004; Potti 2008), but unfortunately, such collections do not exist.

For comparisons between eggs from the field and museum collections, we had the following sampling structure for each of the three species:

Common Guillemot – eggs for the field collection (n = 317) were obtained from Skomer Island, Pembrokeshire, Wales (51.7358° N, 5.2964° W) (under licence) during the 2014-2018 breeding seasons. Where we suspected multiple eggs were from the same female (from different years), we included only one of those eggs in the dataset (selected at random). We found no significant difference in shape between years and therefore pooled data across years (see Supplementary

Material for further information). Museum collection eggs (n = 116) were from the National Museum Wales, collected from several Pembrokeshire guillemot colonies (see Supplementary Material for details). The museum eggs were obtained during the early 20th Century by several collectors. Ringing recoveries (Birkhead 1974; Mead 1974; Lindner 2000) and the lack of strong genetic differentiation and structure between colonies across the North-Atlantic (Riffaut et al. 2005) suggest that Skomer Island and other Pembrokeshire colonies are likely part of a single Irish Sea population and possibly even a North Atlantic population unit (Friesen 1997; Hedrick 2001; Riffaut et al. 2005).

Razorbill – eggs for the field collection (n = 58) were from Skomer Island (under licence) in 2015-2018. The museum collection (n = 86) was from the National Museum Wales, from several Pembrokeshire colonies (see Supplementary Material for further details), obtained during the early to mid-20th Century by several collectors. There were no significant differences in the shape indices between years in the field collection, and so we pooled data across years (see Supplementary Material for further information).

Northern Fulmar – eggs for the field collection (n = 33) were from a colony on the Faeroes (61.8926° N, 6.9118° W) in 2019 during the traditional egg harvest (Jensen 2012). The museum collection (n = 31) was from the Natural History Museum at Tring, also taken from Faeroese colonies between the mid-1800s and early 1900s by several collectors.

Egg shape and size characteristic measurements

We obtained egg volume and three shape indices for all eggs using methods developed by Biggins et al. (2018): (1) *pointedness* (also referred to as asymmetry, e.g. Deeming & Ruta 2014), the length from the maximum breadth to the more distant end divided by the maximum egg length; (2) *elongation*, the ratio of the maximum length to the maximum breadth, and (3) *polar asymmetry*, the ratio of the diameter of the largest circle that can fit within the egg outline touching the egg at its blunt pole to the diameter of the largest circle within the egg outline and touching the more pointed pole.

Statistical analyses

To assess whether there is collection bias in the museum collections, we compared the field and museum collections for each species individually. We compared: [1] the difference in means from the two egg collections using a Welch two-sample *t*-test; [2] the coefficients of variation using the Modified Signed-likelihood Ratio Test (Krishnamoorthy and Lee 2014) using the '*cvequality*' version 0.2.0 R package (Marwick & Krishnamoorthy 2019), and [3] the overall egg sample distributions using a two-sample Kolmogorov–Smirnov test. As each type of statistical analysis involved multiple comparisons – four in total (i.e. pointedness, elongation, polar asymmetry and egg volume) – within each species, there is potential for Type I errors to occur (McDonald 2014). Hence, throughout our statistical analysis we applied a Bonferroni correction to account for these multiple comparisons, so that an adjusted significance level of $\alpha = 0.0125$ (0.05/4) was set.

All statistical analyses were performed using R-statistical software version 3.6.1 (R Core Team 2019).

Results

Sample means

Mean elongation, polar asymmetry, and egg volume did not differ significantly between eggs from field and museum collections for any of the three species ($p > 0.0125$; Table 1 and 2, and Figure 3). However, in the Common Guillemot comparisons only, mean pointedness was significantly higher in the museum collection than the field ($t = 3.93$, df = 200.45, $p < 0.001$; see Table 1 and 2, and Figure 1). There were no such significant differences in mean pointedness between eggs from field and museum collections for Razorbills or Northern Fulmars ($p > 0.0125$; Table 1 and 2, and Figure 1).

Coefficient of variations

The coefficient of variation of eggs from the field and museum collections for polar asymmetry, and egg volume did not significantly differ for any of the three species ($p > 0.0125$; see Table 1 and 2, and Figure 1). For pointedness, the coefficient of variation was found to be significantly greater in eggs from the field collection than the museum collection for Northern Fulmars (MSLRT = 6.96, $p = 0.008$; see Table 1 and 2, and Figure 1), although there were no significant differences in Common

Guillemots and Razorbills ($p > 0.0125$; see Table 1 and 2, and Figure 1). The significant result in the Northern Fulmar was driven by a single egg with an unusually high pointedness score (0.628; also see Figure 1), as excluding this egg resulted in the difference being no longer significant (MSLRT = 3.14, $p = 0.076$). Differences between elongation coefficient of variation for eggs in the field and museum collection was not significant in any of the three species ($p > 0.0125$; Table 1 and 2, and Figure 1).

Sample distributions

The sample distributions for eggs from field and museum collections did not significantly differ for elongation, polar asymmetry, and egg volume for any of the three species ($p > 0.0125$; Table 2 and Figure 1). However, for the Common Guillemot, the sample distributions for pointedness differed significantly ($D = 0.25$, $p < 0.001$; see Table 2), with the museum collection having a more negatively skewed distribution than the field collection (see Figure 1). There were no such significant differences in the sample distributions for pointedness between eggs from field and museum collections for Razorbills or Northern Fulmars ($p > 0.0125$; Table 2 and Figure 1).

Table 1| Mean values (± 95% Confidence Interval) and coefficient of variation (CV) for each of the three shape indices and egg volume for field and museum collections of Common Guillemot, Razorbill and Northern Fulmar eggs

	Mean (± 95% Confidence Interval)[a]		**Coefficient of variation[a]**	
	Field collection	**Museum collection**	**Field collection**	**Museum collection**
Common Guillemot				
(Sample sizes: field = 279, museum = 116)				
Pointedness	0.638 (± 0.002)	0.644 (± 0.003)	2.059	2.211
Elongation	1.644 (± 0.008)	1.641 (± 0.014)	3.937	4.660
Polar Asymmetry	2.429 (± 0.035)	2.392 (± 0.055)	12.205	12.575
Egg Volume	94.578 (± 0.886)	94.506 (± 1.284)	7.952	7.387
Razorbill				
(Sample sizes: field = 58, museum = 86)				
Pointedness	0.598 (± 0.004)	0.599 (± 0.003)	2.490	2.410
Elongation	1.579 (± 0.017)	1.560 (± 0.014)	4.075	4.026
Polar Asymmetry	1.917 (± 0.046)	1.954 (± 0.043)	9.090	10.297
Egg Volume	81.463 (± 1.675)	81.981 (± 1.332)	7.822	7.578
Northern Fulmar				
(Sample sizes: field = 33, museum = 31)				
Pointedness	0.550 (± 0.009)	0.548 (± 0.006)	4.663[b]	2.868
Elongation	1.479 (± 0.027)	1.463 (± 0.022)	5.095	4.177
Polar Asymmetry	1.527 (± 0.102)	1.579 (± 0.078)	18.752	13.432
Egg Volume	96.730 (± 4.103)	97.747 (± 3.748)	11.964	10.453

[a] all values reported in the table have been rounded up to 3 decimal places from originally calculated values.

[b] results reported in the table include outlier value reported in the main text (see Results section). When removed the coefficient of variation becomes 3.971.

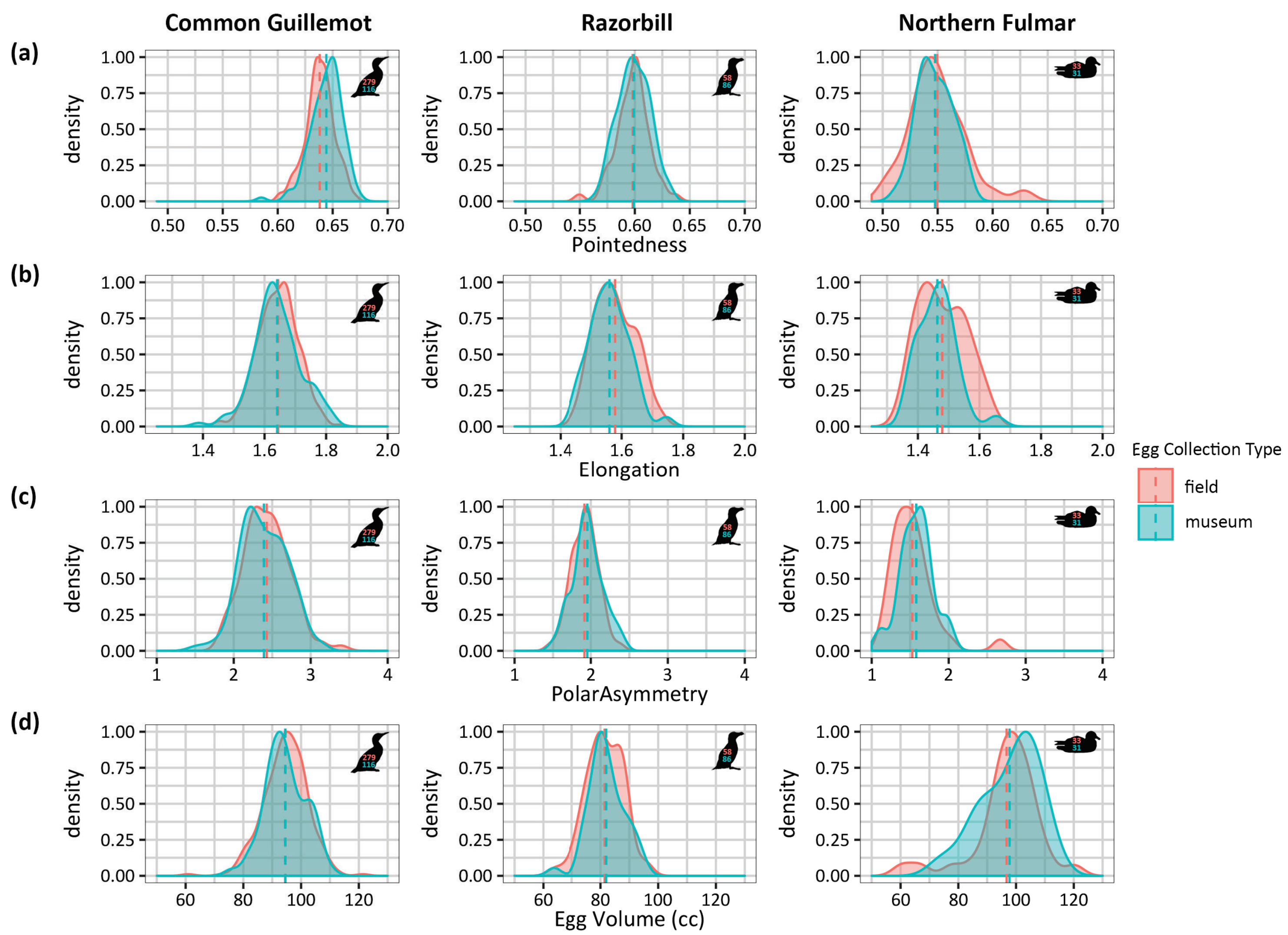


Figure 1| Kernel density plots showing the distribution of egg shape and size measurements in field and museum collections. Dashed coloured lines represent the mean values for the two types of egg collections. All plots had their density axis rescaled so that they are presented on a similar scale of 0-1.

Table 2| Summary table of the statistical tests comparing [1] mean values, [2] coefficient of variation (CV) and [3] sample distributions between Common Guillemot, Razorbill and Northern Fulmar eggs from field and museum collections

	[1] Welch two-sample *t*-test to compare means (*t*-value, degrees of freedom (df), *p*-value[*])	**[2] Modified Signed-Likelihood Ratio Test to compare coefficient of variation** (MSLRT test-value, *p*-value[*])	**[3] Two-sample Kolmogorov-Smirnov Test to compare sample distributions** (*D*-value, *p*-value[*])
Common Guillemot (Sample sizes: field = 279, museum = 116)			
Pointedness	3.93, 200.45, **<0.001**	0.77, 0.38	0.25, **<0.001**
Elongation	0.39, 186.87, 0.70	4.56, 0.03	0.10, 0.38
Polar Asymmetry	1.10, 212.28, 0.27	0.12, 0.73	0.10, 0.39
Egg Volume	0.09, 230.56, 0.93	0.91, 0.34	0.10, 0.38
Razorbill (Sample sizes: field = 58, museum = 86)			
Pointedness	0.41, 119.89, 0.68	0.06, 0.80	0.12, 0.65
Elongation	1.69, 120.48, 0.09	0.01, 0.93	0.16, 0.28
Polar Asymmetry	1.20, 133.34, 0.23	1.06, 0.30	0.14, 0.50
Egg Volume	0.48, 120.34, 0.63	0.06, 0.81	0.11, 0.77
Northern Fulmar (Sample sizes: field = 33, museum = 31)			
Pointedness	0.38, 53.57, 0.70	6.96, **<0.01**[a]	0.12, 0.94
Elongation	0.93, 60.74, 0.35	1.20, 0.27	0.27, 0.16
Polar Asymmetry	0.82, 58.87, 0.41	3.22, 0.07	0.22, 0.36
Egg Volume	0.37, 61.77, 0.71	0.54, 0.46	0.18, 0.56

[*] *p*-values in bold indicate statistical significance ($p < 0.0125$)

[a] when a single extreme egg outlier data point from the field collection is removed and the test is repeated, the result is as follows: 3.14, 0.076

Discussion

We provide evidence of a small but potentially important degree of collection bias in museum egg collections, particularly in species with extreme egg traits. Common Guillemot eggs from the museum collection exhibited greater pointedness than those from the field collection, but were similar in all other respects, whereas Razorbill and Northern Fulmar eggs from museum and field collections did not differ significantly in any of their shape and size traits.

Common Guillemot eggs are characterised by their distinctive pyriform (i.e. pear) shape (Tschanz et al. 1969; Birkhead 1993, 2017; Birkhead et al. 2017a, 2017b; Stoddard et al. 2017). This pyriform shape has intrigued both researchers and the public for many years (see Birkhead 2016, 2017) and numerous studies have examined its possible evolutionary drivers (e.g. Hewitson 1831; Belopol'skii 1961; Tschanz et al. 1969; Ingold 1980; Birkhead et al. 2017a, 2017b, 2018, 2019; Hays & Hauber 2018; also see Birkhead 2016, 2017). Given this long-standing interest in the pyriform shape of Common Guillemot eggs, it is plausible that private collectors were biased, consciously or subconsciously, towards selecting eggs that demonstrate the most extreme pyriform shape. More extreme pyriform eggs are typically associated with increased measures of pointedness/asymmetry (Biggins et al. 2018; but also see Hays & Hauber 2018). Hence, our study's finding of significantly greater pointedness/asymmetry within the museum Common Guillemot egg collection is consistent with the idea that egg collectors' preferences towards extreme pyriform eggs (be it conscious or subconscious) may have driven collection bias.

Another explanation for the differences in the pointedness of museum and field collected Common Guillemot eggs is that these are a consequence of differing selection pressures at different colonies. Avian egg shape traits are genetically heritable (e.g. Kendeigh et al. 1956; Petersen 1992; Mónus & Barta 2005) and potentially result from interactions between genetic and environmental factors (Falconer 1989; Ridley 1993). In Common Guillemots, egg shape traits within female are highly repeatable (Birkhead et al. 2017a) and shape appears to be driven by adaptive selection pressures at the incubation stage (e.g. Birkhead et al. 2017a; 2018, 2019; Hays & Hauber 2018). Any notable differences in selection pressures, particularly at the incubation stage, might therefore result in varying egg shape traits across populations. However, given that eggs from our comparison sets were collected from colonies within the county of Pembrokeshire, which are very likely to be part of the same geographic population unit (Mead 1974; Friesen 1997; Riffaut et al. 2005), it seems unlikely that selection pressures across these different colonies differ. Furthermore, if selection pressures differ between geographic localities, we might expect the other shape traits to also differ. Previous studies have shown multiple shape traits to contribute to specific adaptive functional benefits (e.g. egg stability, Birkhead et al. 2018). However, only pointedness significantly differed between the two egg collections, and so the most parsimonious explanation for the observed differences is the occurrence of collection bias towards more asymmetric eggs.

We hypothesised that the risk of collection bias towards a given egg trait might also increase for species when the natural variation for that trait is higher. Common Guillemot eggs have been previously noted to exhibit considerable variation in shape (Tschanz et al. 1969; Birkhead et al. 2017a). Yet, in our current study the observed variations in the shape and size traits of the field egg collection are somewhat similar to, or even smaller than, those for the Razorbill and Northern Fulmar (Table 1). Whilst it would be of interest to further examine the extent of the consistency in variations for egg shape and size traits across more bird species, evident collection bias in only the Common Guillemot museum egg collections, despite no notably greater variation in shape and size traits, invalidates this hypothesis.

There are two potential limitations to our current study. First, our museum and field egg collections were not sampled at exactly the same locality or the same time, although, as noted above, we believe the comparisons used are still suitably informative for examining collection bias. Second, sample sizes in parts of our dataset were relatively small. Preston (1968) proposed that in order to assess whether the eggs of two populations differ significantly in shape, ‘60 or 100 clutches are desirable’ for comparisons, although he did not specify the basis for these values. Our Common Guillemot sample sizes exceeded this (279 field and 116 museum eggs), thus making the significant differences in pointedness more likely to be true, and our Razorbill samples sizes were similar to those recommended (58 field and 86 museum eggs). However, data for the Northern Fulmar were smaller than this desired sample size (33 field and 31 museum).

Previously, it has been noted how egg collectors sometimes included in their collections unusually small (i.e. dwarf) and large (i.e. double-yolked) eggs (Koenig 1980; Mallory et al. 2004). This is especially apparent in museum collections of Common Guillemot eggs (Birkhead et al. 2017a). Such eggs are usually inviable and are typically the result of pathological issues (e.g. Ingersoll 1910; Curtis

1914; Pearl & Curtis 1916; Conrad and Warren 1940; Romanoff and Romanoff 1949; Fasenko et al. 2000). Because these eggs are unlikely to represent part of the natural variation of biologically viable eggs, they should not be included in studies trying to understand egg shape variations. Fortunately, these eggs are often either noted as dwarf or double-yolked eggs on the data card, and/or are physically separated from other eggs within collections (J.E.T. *per. obs.*). However, this may not always be the case, which raises further complications when assessing biases within museum egg collections. Qualitative or quantifiable size anomalies could be used to identify abnormal eggs. However, without having the necessary information about the inner contents of a particular egg (i.e. confirming whether an egg deemed as a dwarf does in fact lack a yolk, or one deemed to be a double-yolked did actually contain two yolks, as typically observed in these abnormal egg forms – see Curtis 1914; Pearl & Curtis 1916; Romanoff & Romanoff 1949; Koenig 1980), it is difficult to establish whether these eggs are abnormal or whether they are at the extremes within the normal range. This raises the issue (also alluded to by Preston 1968) of when an egg should be considered abnormal/non-viable and excluded from the dataset. Indeed, some researchers have made previous attempts to develop criterion for identifying abnormal eggs within certain species (e.g. dwarf/runt eggs in the Acorn Woodpecker *Melanerpes formicivorus*, Koenig 1980). Future studies should continue to consider and develop appropriate methods to minimise the risk of including abnormal eggs without mistakenly removing viable eggs at the extremities of natural variation.

In conclusion, our results show that collection bias driven by specific shape traits can occur in museum egg collections, and that such bias may be more evident in species that exhibit more extreme egg shapes. Since museum egg collections continue to be an invaluable resource for exploring evolutionary questions about avian egg shape and other traits, our findings highlight the need to fully ascertain the prevalence of bias in study collections and to develop appropriate strategies to remove or reduce such bias.

Acknowledgements

We are very grateful to Douglas Russell at the Natural History Museum at Tring, and Jennifer Gallichan and Julian Carter at the National Museum Wales for their invaluable assistance and support during our use of the egg collections in their care. We thank Sjúrður Hammer of the Umhvørvisstovan, Environment Agency (Faeroes), for providing photographs of field collected Northern Fulmar eggs from the Faeroes. We are grateful to the Wildlife Trust of South and West Wales (and Lizzie Wilberforce in particular) and Natural Resources Wales for permission to work on

Skomer Island and to collect and photograph the eggs. We thank the previous Skomer wardens, Birgitta Buche and Edward Stubbings, and our field assistants for their help. Thanks to Dr Kathryn Maher, Dr Nicola Hemmings and Professor Robert Montgomerie for suggestions and improvements to the manuscript. The study was funded by a grant from the Leverhulme Trust (to T.R.B.).

J.E.T. and T.R.B. conceived the study; J.E.T. wrote the manuscript with contributions from T.R.B.; J.E.T. and T.R.B. collected the data; J.E.T. analysed the data. The authors declare no competing interests.

References in Appendix 1:

Attard, M. R. G., Medina, I., Langmore, N. E., and Sherratt, E. (2017). Egg shape mimicry in parasitic cuckoos. *Journal of Evolutionary Biology*, **30**, 2079-2084.

Belopol'skii, L. O. (1961). *Ecology of Sea Colony Birds of the Barents Sea.* (translated from original 1957 publication by Ettinger R. and Salzmann C.). Israel Program for Scientific Translations: Jerusalem.

Biggins, J. D., Thompson, J. E. and Birkhead, T. R. (2018). Accurately quantifying the shape of birds' eggs. *Ecology and Evolution*, **8**, 9728-9738.

Birkhead, T. R. (1974). Movement and Mortality Rates of British Guillemots. *Bird Study*, **21**, 241-254.

Birkhead, T. R. (1977). The Effect of Habitat and Density on Breeding Success in the Common Guillemot (*Uria aalge*). *Journal of Animal Ecology*, **46**, 751-764.

Birkhead, T. R. (1993). *Great Auk Islands: A Field Biologist in the Arctic.* Poyser: London.

Birkhead, T. R. (2016). *The Most Perfect Thing: The Inside (and Outside) of a Bird's Egg.* Bloomsbury: London.

Birkhead, T. R. (2017). Vulgar errors: the point of a Guillemot's egg, or why the widely believed explanation for the guillemot's pointed egg is almost certainly wrong. *British Birds*, **110**, 456-467.

Birkhead, T. R. and Montgomerie, R. (2018). Rare red eggs of the Common Guillemot (*Uria aalge*): birds, biology and people at Bempton, Yorkshire, in the early 1900s. *Archives of Natural History*, **45**, 69-79.

Birkhead, T. R., Thompson, J. E. and Biggins, J. D. (2017a). Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: not a rolling matter? *Journal of Ornithology*, **158**, 679-685.

Birkhead, T. R., Thompson, J. E., Jackson, D. and Biggins, J. D. (2017b). The point of a Guillemot's egg. *Ibis*, **159**, 255-265.

Birkhead, T. R., Thompson, J. E. and Montgomerie, R. (2018). The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *The Auk*, **135**, 1020-1032.

Birkhead, T. R., Thompson, J. E., Biggins, J. D. and Montgomerie, R. (2019). The evolution of egg shape in birds: selection during the incubation period. *Ibis*, **161**, 605-618.

Cassey, P., Portugal, S. J., Maurer, G., Ewen, J. G., Boulton, R. L., Hauber, M. E. and Blackburn, T. M. (2010a). Variability in Avian Eggshell Colour: A Comparative Study of Museum Eggshells. *PLoS ONE*, **5**, e12054.

Cassey, P., Maurer, G., Duval, C., Ewen, J. G. and Hauber, M. E. (2010b). Impact of time since collection on avian eggshell color: a comparison of museum and fresh egg specimens. *Behav. Ecol. Sociobiol.*, **64**, 1711–1720.

Cherry, M. I. and Gosler, A. G. (2010). Avian eggshell coloration: new perspectives on adaptive explanations. *Biological Journal of the Linnean Society*, **100**, 753-762.

Christians, J. K. (2002). Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews*, **77**, 1-26.

Conrad, R. M. and Warren, D. C. (1940). The production of double yolked eggs in the fowl. *Poultry Science*, **19**, 9–17.

Curtis, M. R. (1914). Studies on the physiology of reproduction in the domestic fowl-VI. Double- and triple-yolked eggs. *The Biological Bulletin*, **26**, 55-83.

Deeming, D. C. (2018). Effect of composition on shape of bird eggs. *Journal of Avian Biology*, **49**, e01528.

Deeming, D. C. and Ruta, M. (2014). Egg shape changes at the theropod-bird transition, and a morphometric study of amniote eggs. *Royal Society Open Science*, **1**, 140311.

Duursma, D. E., Gallagher, R. V., Price, J. J. and Griffith, S. C. (2018). Variation in avian egg shape and nest structure is explained by climatic conditions. *Scientific Reports*, **8**, 4141.

Falconer, D. S. (1989). *Introduction to quantitative genetics*. Longmann: Harlow.

Fasenko, G. M., Robinson, F. E., Danforth, B. L. and Zelter, I. (2000). An examination of fertility, hatchability, embryo mortality, and chick weight in double versus single-yolked broiler breeder eggs. *Canadian Journal of Animal Science*, **80**, 489-493.

Friesen, V. L. (1997). Population genetics and the spatial scale of conservation of colonial waterbirds. *Colon. Waterbirds*, **20**, 353–368.

Gaston, A. J. and Nettleship, D. N. (1981). *The Thick-billed Murres of Prince Leopold Island.* Canadian Wildlife Service Monographs, No. 6: Ottawa.

Grealy, A., Bunce, M. and Holleley, C. E. (2019). Avian mitochondrial genomes retrieved from museum eggshell. *Molecular Ecology Resources*, **19**, 1052-1062.

Green, R. E. (1998). Long-term decline in the thickness of eggshells of thrushes, *Turdus* spp., in Britain. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 679-684.

Harris, M. P. and Birkhead, T. R. (1985). Breeding ecology of the Atlantic Alcidae. In: *The Atlantic Alcidae.* (eds. Nettleship, D. N. and Birkhead, T. R.). Academic Press: London. pp. 155-205.

Hauber, M. E., Bond, A. L., Kouwenberg, A-L., Robertson, G. J., Hansen, E. S., Holford, M., Dainson, M., Luro, A. and Dale, J. (2019). The chemical basis of a signal of individual identity: shell pigment concentrations track the unique appearance of Common Murre eggs. *Journal of the Royal Society Interface*, **16**, 20190115.

Hays, I. R. and Hauber, M. E. (2018). How the egg rolls: a morphological analysis of avian egg shape in the context of displacement dynamics. *Journal of Experimental Biology*, **221**, jeb178988.

Hedrick, P. W. (2001). Conservation genetics: where are we now? *Trends in Ecology and Evolution*, **16**, 629–636.

Hendricks, P. (1991). Repeatability of size and shape of American Pipit eggs. *Canadian Journal of Zoology*, **69**, 2624-2628.

Hewitson, W. C. (1831). *British oology: being illustrations of the eggs of British birds, with figures of each species, as far as practicable, drawn and coloured from nature: accompanied by descriptions of the materials and situation of their nests, number of eggs.* Empson: Newcastle upon Tyne.

Hickey, J. J. and Anderson, D. W. (1968). Chlorinated Hydrocarbons and Eggshell Changes in Raptorial and Fish-Eating Birds. *Science*, **162**, 271-273.

Ingersoll, A. M. (1910). Abnormal Birds' Eggs. *Condor*, **12**, 15-17.

Ingold, P. (1980). Anpassungen der Eier und des Brutverhaltens von Trottellummen (*Uria aalge aalge* Pont.) an das Brüten auf Felssimsen. *Zeitschrift für Tierpsychologie*, **53**, 341-388.

Jensen, J-K. (2012). *Mallemukken på Færøerne*. [The Fulmar on the Faroe Islands]. Prenta: Torshavn.

Kendeigh, S. C., Kramer, T. C. and Hamerstrom, F. (1956). Variations in Egg Characteristics of the House Wren. *The Auk*, **73**, 42-65.

Kilner, R. M. (2006). The evolution of egg colour and patterning in birds. *Biological Reviews*, **81**, 383-406.

Koenig, W. D. (1980). The Determination of Runt Eggs in Birds. *The Wilson Bulletin*, **92**, 103-107.

Krishnamoorthy, K. and Lee, M. (2014). Improved tests for the equality of normal coefficients of variation. *Computational Statistics*, **29**, 215-232.

Lack, D. (1946). Clutch and brood size in the robin. *British Birds*, **39**, 98–109, 130–135.

Lindner, R. (2000). *The Population Biology of the Common Guillemot, Uria aalge*. PhD Thesis, University of Sheffield.

Mallory, M. L., Kiff, L., Clark, R. G., Bowman, T., Blums, P., Mednis, A. and Alisauskas, R. T. (2004). The occurrence of runt eggs in waterfowl clutches. *Journal of Field Ornithology*, **75**, 209-217.

Mänd, R. and Tilgar, V. (2003). Does supplementary calcium reduce the cost of reproduction in the Pied Flycatcher *Ficedula hypoleuca*? *Ibis*, **145**, 67-77.

Marwick, B. and Krishnamoorthy, K. (2019). *cvequality: Tests for the Equality of Coefficients of Variation from Multiple Groups. R package version 0.2.0*. Available at: https://CRAN.R-project.org/package=cvequality

Mead, C. J. (1974). The Results of Ringing Auks in Britain and Ireland. *Bird Study*, **21**, 45-86.

McDonald, J. H. (2014). *Handbook of Biological Statistics (3rd ed.)*. Baltimore: Sparky House Publishing. Maryland.

McNair, D. B. (1987). Egg data slips: Are they useful for information on egg-laying dates and clutch size? *The Condor*, **89**, 369–376.

Mónus, F. and Barta, Z. (2005). Repeatability Analysis of Egg Shape in a Wild Tree Sparrow (*Passer montanus*) Population: A Sensitive Method for Egg Shape Description. *Acta Zoologica Academiae Scientiarum Hungaricae*, **51**, 151-162.

Moreno, J., Lobato, E. and Morales, J. (2011). Eggshell blue-green colouration fades immediately after oviposition: a cautionary note about measuring natural egg colours. *Ornis Fennica*, **88**, 51–56.

Newton, A. V. (1896). *A dictionary of birds.* A and C Black: London.

Newton, I., Bogan, J., Meek, E. and Little, B. (1982). Organochlorine compounds and shell-thinning in British Merlins *Falco columbarius*. *Ibis*, **124**, 328-335.

Pearl, R. and Curtis, M. R. (1916). Studies on the physiology of reproduction in the domestic fowl-XV. Dwarf eggs. *Journal of Agricultural Research*, **6**, 977-1042.

Petersen, M. R. (1992). Intraspecific Variation in Egg Shape among Individual Emperor Geese (Variación Intraespecífica en la Forma de los Huevos de Chen canagicus). *Journal of Field Ornithology*, **63**, 344-354.

Potti, J. (2008). Temperature during egg formation and the effect of climate warming on egg size in a small songbird. *Acta Oecologica*, **33**, 387-393.

Preston, F. W. (1968). The shapes of birds' eggs: Mathematical aspects. *The Auk*, **85**, 454-463.

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Ratcliffe, D. A. (1967). Decrease in Eggshell Weight in Certain Birds of Prey. *Nature*, **215**, 208-210.

Ridley, M. (1993). *Evolution*. Blackwell Science: Boston.

Riffaut, L., McCoy, K. D., Tirard, C., Friesen, V. L. and Boulinier, T. (2005). Population genetics of the common guillemot *Uria aalge* in the North Atlantic: geographic impact of oil spills. *Marine Ecology Progress Series*, **291**, 263-273.

Romanoff, A. L. and Romanoff, A. J. (1949). *The Avian Egg.* John Wiley & Sons, Inc.: New York.

Schönwetter, M. (1960-1992). *Handbuch der Oologie*. Akademie Verlag: Berlin.

Shatkovska, O. V., Ghazali, M., Mytiai, I. S. and Druz, N. (2018). Size and shape correlation of birds' pelvis and egg: Impact of developmental mode, habitat, and phylogeny. *Journal of Morphology*, **279**, 1590-1602.

Spottiswoode, C. N. and Stevens, M. (2011). How to evade a coevolving brood parasite: egg discrimination versus egg variability as host defences. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3566-3573.

Starling, M., Heinsohn, R., Cockburn, A. and Langmore, N. E. (2006). Cryptic gentes revealed in pallid cuckoos *Cuculus pallidus* using reflectance spectrophotometry. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1929–1934.

Stevens, M. (2011). Avian vision and egg colouration: concepts and measurements. *Avian Biology Research*, **4**, 168-184.

Stoddard, M. C. and Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1387-1393.

Stoddard, M. C., Kilner, R. M. and Town, C. (2014). Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. *Nature Communications*, **5**, 4117.

Stoddard, M. C., Yong, E. H., Akkaynak, D., Sheard, C., Tobias, J. A. and Mahadevan, L. (2017). Avian egg shape: Form, function and evolution. *Science*, **356**, 1249-1254.

Stoddard, M. C., Hogan, B. G., Stevens, M. and Spottiswoode, C. N. (2019a). Higher-level pattern features provide additional information to birds when recognizing and rejecting parasitic eggs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **374**, https://doi.org/10.1098/rstb.2018.0197

Stoddard, M. C., Sheard, C., Akkaynak, D., Yong, E. H., Mahadevan, L. and Tobias, J. A. (2019b). Evolution of avian egg shape: underlying mechanisms and the importance of taxonomic scale. *Ibis*, **161**, 922-925.

Swynnerton, C. F. M. (1916). On the Coloration of the Mouths and Eggs of Birds. – II. On the Coloration of Eggs. *Ibis*, **4**, 529-606.

Thompson, D'A. W. (1917). *On Growth and Form.* Cambridge University Press: Cambridge.

Thomson, A. L. (1964). *A New Dictionary of Birds.* Nelson: London.

Trobe, W. M. and Whitaker, J. (2014). *Red eggs – erythristic eggs of the Corvidae*. Peregrine Books: Leeds.

Tryjanowski, P., Sparks, T. H., Kuczyński, L. and Kuźniak, S. (2004). Should avian egg size increase as a result of global warming? A case study using the red-backed shrike (*Lanius collurio*). *Journal of Ornithology*, **145**, 264-268.

Tschanz, B., Ingold, P. and Lengacher, H. (1969). Eiform und Bruterfolg bei Trottellummen (*Uria aalge*). *Ornithologische Beobachter*, **66**, 25-42.

Underwood, T. J. and Sealy, S. G. (2002). Adaptive significance of egg coloration. In: *Avian Incubation: Behaviour, Environment and Evolution* (ed. Deeming, D. C.). Oxford University Press: Oxford. pp. 280-298.

Väisänen, R. A. (1969). Evolution of the ringed plover (*Charadrius hiaticula* L.) during the last hundred years in Europe. A new computer method based on egg dimensions. *Annales Academiae Scientiarum Fennicae Series A: IV, Biologica*, **149**, 1–90.

Wallace, A. R. (1889). *Darwinism: An exposition of the theory of natural selection with some of its applications.* Macmillan and Co.: London.

Walters, M. (1994). *Birds' Eggs.* Dorling Kindersley: London.

Supplementary Information for Appendix 1

Common Guillemot and Razorbill museum collection information

The Common Guillemot museum collection eggs (n = 116) were from the National Museum Wales and consisted of eggs from the following colonies within the county of Pembrokeshire:

'Pembrokeshire Islands' (n = 7)

Skomer Island (n = 3)

Ramsey Island (n = 7)

Grassholm (n = 11)

'Caraig Rasson, Pembrokeshire' (n = 28)

North Bishop (n = 60)

The Razorbill museum collection eggs (n = 86) were from the National Museum Wales and consisted of eggs from the following colonies within the county of Pembrokeshire:

North Bishop (n = 42)

'Caraig Rasson, Pembrokeshire' (n = 8)

'Pembrokeshire Islands' (n = 10)

Ramsey Island (n = 20)

Skomer Island (n = 3)

Grassholm (n = 3)

Comparisons of shape indices between breeding seasons for the Common Guillemot and Razorbill field egg collections

Comparing Common Guillemot eggs collected on Skomer Island during the 2014-2018 breeding seasons, we found no significant differences in the mean pointedness (ANOVA: $F_{(4,\ 274)} = 0.91$, p =

0.46), elongation (ANOVA: $F_{(4,\ 274)} = 1.57$, $p = 0.18$) and polar asymmetry (ANOVA: $F_{(4,\ 274)} = 0.63$, $p = 0.64$) across different breeding seasons. Similarly, we found no significant differences in the mean pointedness (ANOVA: $F_{(3,\ 54)} = 1.17$, $p = 0.33$), elongation (ANOVA: $F_{(3,\ 54)} = 0.41$, $p = 0.74$) and polar asymmetry (ANOVA: $F_{(3,\ 54)} = 0.51$, $p = 0.68$) between Razorbill eggs collected across the 2015-2018 breeding seasons.

APPENDIX 2:

Two-egg clutches in the Fulmar

Two-egg clutches in the Fulmar

Birkhead, T. R., Jensen, J-K., Thompson, J. E., Hammer, S., Thompson, P. and Montgomerie, R.
(2020). *British Birds*, **113**, 165-170.

Original article can be found using the link below:
https://britishbirds.co.uk/article/two-egg-clutches-in-the-fulmar/

This article has been reproduced in this thesis with direct permission from Roger Riddington, editor of British Birds.

Paper context and thesis author's contributions: The Northern Fulmar *Fulmarus glacialis* typically produces a single-egg clutch, yet there have been previous observations of apparent two-egg clutches produced within this species. Whilst there have been a number of recorded cases of two-egg clutches within Northern Fulmar, it is not clear whether or not these eggs have in fact been laid by the same female. Given that there is typically high repeatability for shape traits in eggs laid by the same female, this study used methods presented in **Chapter 2** to quantify shape and compare the shape differences between eggs from the two-egg clutches and those of eggs randomly paired together in order to ascertain the likelihood of whether or not the same female laid both eggs within sampled two-egg clutches.

My contribution to this published article comprised of processing previously obtained egg photos for eggs from the two-egg clutches and previously harvested eggs from a Faroes colony and then performing all the automated shape analysis script runs and collating part of the data used in the study. I provided the idea that whilst egg shape traits appeared to be not repeatable in the two-egg clutches, it is possible (although unlikely) that the same female might have laid both eggs through a pathological condition that results in two dissimilar eggs being produced. I also contributed suggestions and improvements to re-drafts of the manuscript.

Co-authors' contributions: T.R. Birkhead did the research for the study and wrote the initial draft of the manuscript. J-K. Jensen provided the two-egg clutches sampled in the study. S. Hammer photographed and measured eggs from the two-egg clutches and those previously harvested in the Faroes. P.M. Thompson collated and provided a long-term dataset for a Northern Fulmar colony in Eynhallow, Orkney that contained egg measurements for eggs laid by the same females across multiple breeding years. R. Montgomerie performed all the statistical analyses and produced the figures presented in the paper. All co-authors contributed suggestions and improvements to subsequent re-drafts of the manuscript.

Two-egg clutches in the Fulmar

Tim Birkhead, Jens-Kjeld Jensen, Jamie Thompson, Sjúrður Hammer, Paul Thompson and Robert Montgomerie

Abstract Members of the seabird family Procellariidae (albatrosses, petrels and shearwaters) typically produce a single-egg clutch. Two-egg clutches have been recorded occasionally in some of those species, but it is not known whether they were laid by a single female. In this study we examined eight two-egg clutches of the Fulmar *Fulmarus glacialis* in the Faroes, to assess whether those eggs may have been laid by the same female. Using data from eggs laid in different years by the same 100 females on Eynhallow, Orkney, we first confirmed that the egg measurements were repeatable from year to year. Second, using egg length, breadth, volume and three indices of shape, we compared the eggs from the eight two-egg clutches with (i) 100 pairs of eggs sampled at random from 111 single-egg clutches from the Faroes, and (ii) eggs laid in different years by 100 females on Eynhallow. Our analyses focused on differences between eggs in each pair. Differences in the eggs of two-egg clutches were more similar to those of pairs of eggs taken at random than to pairs of eggs from the same female in different years. We infer from this that the eggs in two-egg clutches were laid by different females.

All Procellariiformes (albatrosses, petrels, shearwaters) typically produce a single-egg clutch (Warham 1990), but occasionally two eggs occur at the same nest site. Although it is often assumed that these are laid by two different females (Warham 1990; Ryan *et al.* 2007), it has occasionally been asserted that the two eggs were laid by the same female (reviewed in Tickell & Pinder 1966).

The incidence of two-egg clutches in populations of the Fulmar *Fulmarus glacialis* varies from zero to around 15%. Lockley (1936) reported that in the Vestmannaeyjar (Westmann Islands), Iceland, 10–15% of Fulmar nest sites contained two eggs, although for the same locality Einarsson (cited in Fisher 1952) reported a much lower incidence, of 1.6% (67/4,150 nest sites). Similarly, Jensen (1989) reported that 0.82% (25/3,047) of Fulmar nest sites on the Faroes contained two eggs. He suggested that these were laid by the same female because: (i) the eggs were similar in shape (assessed visually); and (ii) at one nest site, two eggs had been found in four consecutive years. On the other hand, Fisher (1952), commenting on two-egg clutches in this species, wrote:

> In 1947, on a holm in West Shetland, the oologist *Peregrine* [Frank Watmough – Jim Whitaker, pers. comm.] found one of the rare two-egg clutches of the Fulmar. 'One egg was very long' he writes, 'and the other much more round' and… On landing at the same place in 1948 'lo and behold, the Fulmar was in the self-same spot and again with two eggs, one long and the other round' (Birdland 1948).

The most obvious ways to establish whether or not two-egg clutches in the

Jens-Kjeld Jensen

55. Participants in the traditional Faroes harvest of Fulmar *Fulmarus glacialis* eggs for human consumption, in May 2010.

Fulmar are laid by the same or two different females would be: (i) to witness the eggs being laid by individually recognisable females (which would be very difficult, but see Tickell & Pinder 1966); or (ii) to use molecular techniques to ascertain the maternity of both eggs by obtaining DNA from the shell membrane, from the shell itself or from the developing chicks (Grealy *et al.* 2019). It is easier to establish that two eggs or offspring have different mothers than it is to demonstrate that they have the same mother, but molecular analyses of either type require: (i) DNA from both the focal eggs and the putative mother as well as the general Fulmar population; (ii) considerable technical skill; (iii) sufficient financial resources to undertake the analyses; and (iv) a sufficient number of molecular markers (Waits *et al.* 2001; Jones & Ardren 2003).

An additional method that may allow us to distinguish between the two hypotheses is to compare the dimensions and shape of eggs in two-egg clutches on the well-verified assumption that individual females typically lay eggs more similar in shape, volume and linear dimensions than two eggs laid by different females (Romanoff & Romanoff 1949; Petersen 1992 and references therein; Mónus & Barta 2005; Birkhead *et al.* 2017). Thus, we predicted that, if the eggs in two-egg clutches were laid by the same female, they would be less different in all or most of the six size and shape traits than pairs of eggs taken at random from the population.

Methods

The traditional Faroes harvest of Fulmar eggs for human consumption is still undertaken (Jensen 2012) and this local access can provide important insights into the breeding biology of Fulmars. Although two-egg clutches in Fulmars on the Faroes have been known to occur historically, and at low frequency, in 2019 local egg-collectors noted that among 34 clutches found in Byrgisgjógv, Sandavágur, there were five or six two-egg clutches, while on Lonin, Sandoy, collectors reported approximately 15 two-egg clutches among 1,600 eggs.

In 1988 and 1989, JKJ enlisted the assistance of close friends involved in the traditional Faroes Fulmar egg harvest to collect any two-egg Fulmar clutches they encountered. A total of eight two-egg clutches was collected, with each pair of eggs placed immediately in a sealed bag and kept separate from the other Fulmar eggs. These eggs from the two-egg clutches were later labelled in pencil and then emptied, washed and dried and retained by JKJ. In 2019, we measured (to the nearest 0.1 mm) the maximum length and breadth of these eggs using Vernier calipers and photographed them individually under standardised conditions (see Biggins *et al.* 2018). From these photographs (fig. 1), we used the method described in Biggins *et al.* (2018) to quantify the volume and three shape parameters – elongation, pointedness (sometimes called asymmetry) and polar asymmetry – of each egg. Elongation is length/width; pointedness is the degree to which the maximum width of the egg deviates from the midpoint of its length; and polar asymmetry is a measure of the relative size of the two ends of the egg.

To assess whether the eggs from the two-egg Fulmar clutches were more similar to each other than was the case for pairs of eggs taken from other females, we made two comparisons. First, we compared those eggs to pairs of randomly chosen eggs from the same Faroes population. To do this we photographed and quantified (as described above) 111 Fulmar eggs collected haphazardly during 17th–21st May 2019. To simulate two-egg clutches from this sample, we randomly chose two eggs (without replacement) and repeated this 100 times with replacement. If the two eggs in real two-egg clutches were laid by the same female, we would expect them to be more similar, on average, than two eggs that were each selected from a different, randomly chosen female.

Second, we compared the eggs in real clutches to two eggs laid by the same female in different years. To do this, we analysed the measurements of 200 eggs laid by 100 individually marked females from the long-term study of Fulmars on Eynhallow, Orkney (Michel *et al.* 2003). These data comprised linear measurements of eggs laid by the same marked females in different, though not always consecutive years, during the periods 1975–84 and 2002–05. All but two of the birds laid the two eggs within one of those periods (mean 3 years), but the eggs from two females were collected 18 and 23 years apart. When their second egg was collected, these 100 females were 1–35 years (mean 10.8 years) after their age of first breeding. We used the egg length and breadth to calculate both volume (using the formula in Michel & Thompson 2003) and elongation. We did not have standardised photographs of Eynhallow Fulmar eggs so we were not able to quantify pointedness or polar asymmetry. If the two eggs in two-egg clutches were laid by the same female, we would expect them to be as similar to each other, on average, as two eggs laid by the same female in different years.

We created 100 simulated clutches from the Faroes to match the sample of paired Eynhallow eggs so that the statistical comparisons between the real two-egg clutches and the other two samples would have similar power. We compared the median of the real two-egg clutches to the medians of the other two samples using separate nonparametric Wilcoxon tests to avoid any issues with outliers and non-normal distributions (see fig. 2).

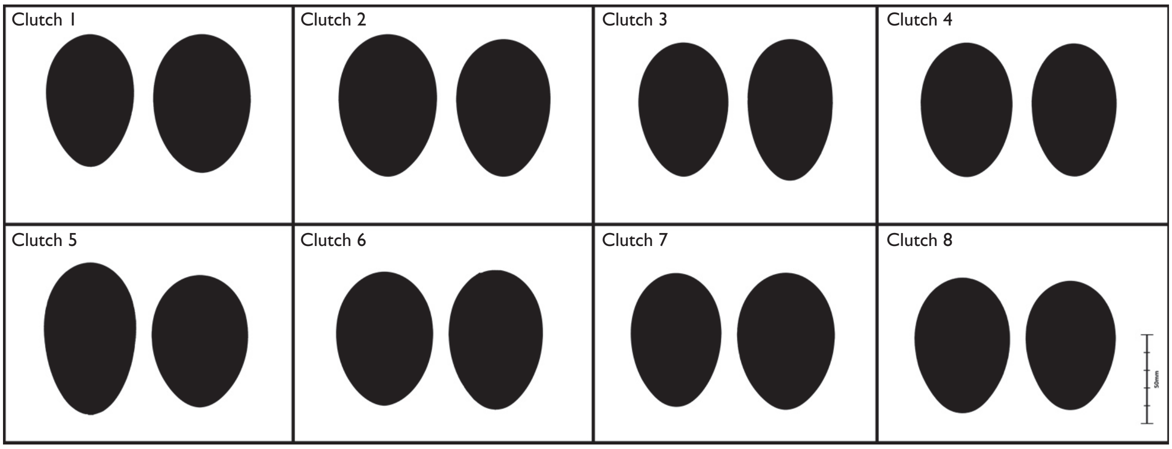


Fig. 1. Silhouettes of the eight pairs of Fulmar *Fulmarus glacialis* eggs collected from the Faroes in 1988–89. The eggs are photographed correctly for shape analysis (see text) and are to scale.

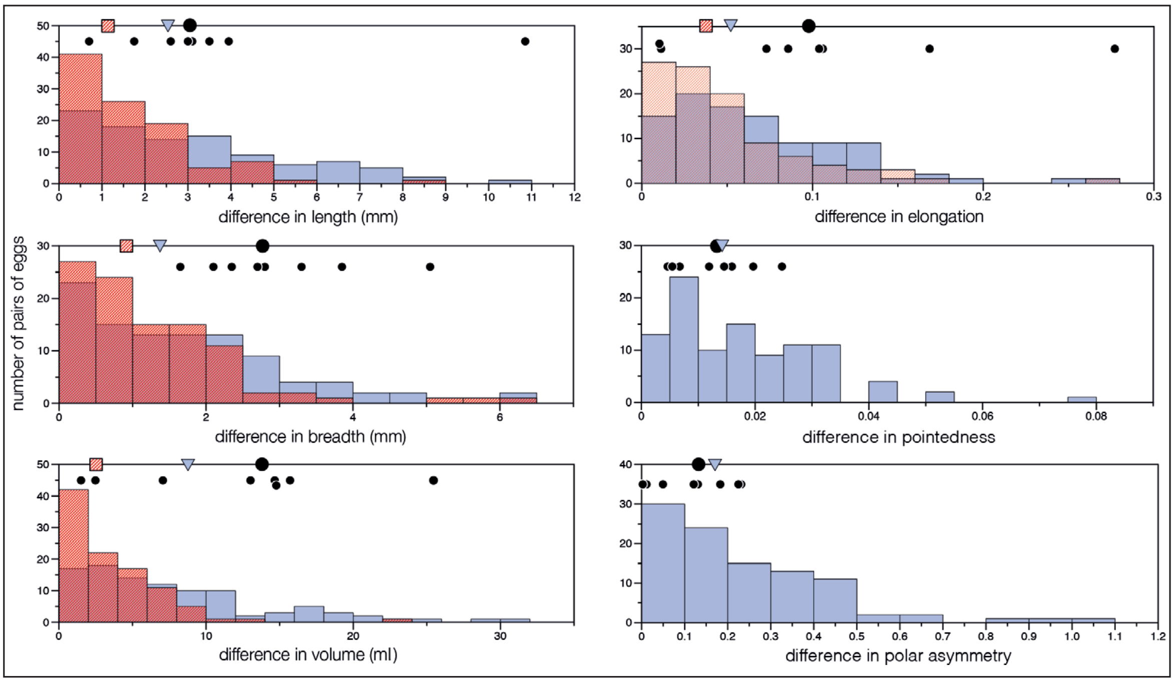


Fig. 2. Differences between pairs of eggs in eight real two-egg Fulmar clutches from the Faroes (black circles), 100 simulated clutches with each egg chosen from a random female on the Faroes (solid blue bars and triangles), and 100 pairs of eggs laid by females in different years on Eynhallow (hatched red bars and squares). Symbols on the top axis of each graph indicate medians (see table 3).

Results

Pairs of eggs laid by the same female on Eynhallow provide some insights into the extent of within-female variation in egg size and shape. The measurements of these eggs were significantly repeatable within females, with repeatabilities ranging from moderate (0.50) to high (0.75) (table 1). None of these egg measurements varied significantly with the year of laying ($r = -0.04–0.08$, $P = 0.29–0.43$, $n = 200$), or the age of the laying female (relative to age of first breeding) for the second egg measured ($r = -0.08–0.05$, $P = 0.36–0.76$, $n = 100$). Nor did the differences between any of the measurements of the two eggs vary significantly with the number of years between the laying of the first and second egg measured ($r = -0.04–0.11$, $P = 0.29–0.68$, $n = 100$).

Eggs from Eynhallow were significantly smaller than those from the Faroes, although the mean differences were slight and there was no significant difference in elongation (table 2). Furthermore, correla-

Table 1. Repeatability of egg measurements from eggs laid in two different years by each female Fulmar *Fulmarus glacialis* on Eynhallow, Orkney (n=100). Confidence limits calculated by bootstrapping; P-value (from likelihood ratio test) tests whether repeatability is different from zero.

variable	repeatability	95% CL	P
length (mm)	0.75	0.65–0.83	<0.0001
breadth (mm)	0.50	0.34–0.64	<0.0001
volume (ml)	0.70	0.59–0.79	<0.0001
elongation	0.59	0.45–0.71	<0.0001

Table 2. Mean [95% CL] measurements of 16 Fulmar eggs in real two-egg clutches on the Faroes (n = 8 clutches), 111 random eggs collected in the Faroes and 200 eggs laid in different years by the same 100 females on Eynhallow, Orkney. For each variable, means with same letter superscript are not significantly different (Tukey posthoc tests from linear models).

variable	two-egg clutches	Faroes	Eynhallow
length (mm)	73.7^{ab} [73.1–74.0]	74.4^{a} (74.0–75.0]	73.6^{b} [73.1–74.0]
breadth (mm)	50.0^{ab} [48.7–51.2]	50.7^{a} [50.4–51.0]	49.7^{b} [49.5–50.0]
volume (ml)	95.1^{a} [89.6–100.6]	99.5^{b} [98.1–100.9]	97.2^{a} [96.3–98.1]
elongation	1.48^{a} [1.43–1.52]	1.46^{a} [1.45–1.48]	1.48^{a} [1.47–1.49]

Table 3. Differences in measurements between the two eggs in eight real two-egg Fulmar clutches on the Faroes, 100 pairs of eggs taken at random from the Faroes, and 100 pairs of eggs from the same female on Eynhallow in different years. Values in parentheses are P-values from Wilcoxon tests for comparisons with the two-egg clutches.

variable	two-egg clutches	Faroes	Eynhallow
length (mm)	3.05	2.30 (0.29)	1.15 (0.008)
breadth (mm)	2.75	1.63 (0.0002)	0.90 (0.0001)
volume (ml)	13.84	8.22 (0.18)	2.60 (0.002)
elongation *	0.095	0.065 (0.09)	0.039 (0.045)
pointedness	0.013	0.015 (0.37)	–
polar asymmetry	0.130	0.23 (0.04)	–

* Note that elongation, pointedness and polar asymmetry are dimensionless values (see Biggins *et al.* 2018).

Table 4. Mean [95% CL] differences in measurements between the two eggs in real two-egg clutches on the Faroes (n = 8 clutches), in two eggs sampled at random from the Faroes (n = 100 pairs of eggs), and in two eggs laid in different years by the same female on Eynhallow (n = 100 pairs of eggs). For each variable, means with same letter superscript are not significantly different (linear models, with length and breadth log10-transformed to normalise residuals).

variable	two-egg clutches	Faroes	Eynhallow
length (mm)	3.68^{a} [1.11–6.25]	2.99^{ab} [2.52–3.45]	1.58^{b} (1.30–1.87)
breadth (mm)	2.98^{a} [2.07–3.88]	1.81^{b} [1.53–2.10]	1.21^{c} [0.99–1.43]
volume (ml)	11.83^{a} [5.24–18.43]	8.25^{ab} [7.04–9.46]	3.58^{b} [2.91–4.26]
elongation	0.10^{a} [0.03–0.18]	0.07^{ab} [0.06–0.08]	0.05^{b} [0.04–0.06]
pointedness	0.013^{a} [0.007–0.019]	0.017^{a} [0.015–0.020]	–
polar asymmetry	0.119^{a} [0.043–0.195]	0.258^{b} [0.219–0.296]	–

tions between the differences between eggs laid by the same female and their mean size measurements were small and not significant (for max. length r = 0.07, P = 0.48; for max. breath r = -0.20, P = 0.09; for volume, r = -0.18, P = 0.08; n = 100 pairs of eggs from Eynhallow). Thus, comparisons of differences between the sizes and shapes of pairs of eggs from the Faroes and Eynhallow populations should not have been influenced by the small mean differences in the overall size of their eggs.

The differences (with respect to length, breadth, volume and elongation) between the two eggs in real two-egg clutches were significantly larger than the differences between two eggs from the same female from Eynhallow (table 3, fig. 2). With one exception (maximum breadth), the median differences in size and shape between the eggs in the real two-egg clutches were not significantly larger than the differences between eggs in the simulated two-egg clutches from the Faroes (table 3, fig. 2). Note also that, with respect to each of these differences within pairs of eggs, the real clutches are more similar to the randomly chosen pairs of eggs than they are to the eggs laid by the same females on Eynhallow (tables 3 & 4). Overall, these results suggest that the eggs in the eight two-egg clutches from the Faroes were laid by different females.

Discussion

The data from individually marked female Fulmars on Eynhallow confirmed that individual females lay eggs of similar linear dimensions, volume and elongation in different years. Significant repeatabilities show that eggs laid by the same female were more similar than the measurements of randomly chosen pairs of eggs from the same population.

For the two-egg clutches on the Faroes, the fact that these were more different than pairs of eggs laid by the same female in different years on Eynhallow is consistent with the idea that the two eggs in the eight Faroes clutches were laid by different females. This conclusion is further supported by the similarity of differences between eggs in the real and simulated two-egg clutches from the Faroes (table 3).

There is a further, albeit remote, possibility, which is that a Fulmar laying two eggs in the same season does so as the result of a pathological condition that also results in the two eggs being dissimilar in size and shape.

Future researchers may be able to use molecular techniques to further investigate this. While it is certainly possible that any of the two-egg clutches could have been laid by the same female, the most parsimonious conclusion, based on our analyses and knowledge of the breeding biology of this species, is that they were laid by different females.

If two-egg clutches are the product of two females, it remains to be explained why this occurs. There are several possibilities: (i) two monogamously paired females both 'assume' that they own the egg-laying site, and in some cases do so in consecutive years; (ii) egg-dumping, or intraspecific brood parasitism, in which a female deliberately deposits an egg in another's nest to avoid the energetic cost of rearing the chick (although in species laying a single egg and only ever rearing a single chick, egg-dumping seems unlikely); and (iii) some Fulmars form female-female pairs (a situation that occurs in some Laysan Albatrosses *Phoebastria immutabilis* and some gull and tern species) and produce supernormal clutches, some of which contain fertile eggs. As in Laysan Albatrosses (Young *et al.* 2008) and these gulls and terns (Hunt & Hunt 1977; Conover *et al.* 1979), the eggs in some two-egg Fulmar clutches on the Faroes contained developing embryos (Jensen 1989).

Acknowledgments

We thank Poul Johannes Simonsen for collecting the two-egg clutches, John Biggins for statistical advice and Jon Slate for comments on the manuscript. The study was funded by a grant from the Leverhulme Trust to TRB.

References

Biggins, J. D., Thompson, J. E., & Birkhead, T. R. 2018. Accurately quantifying the shape of birds' eggs. *Ecol. & Evol.* 8: 9728–9738.
Birkhead, T. R., Thompson, J. E., & Biggins, J. D. 2017. Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: Not a rolling matter? *J. Orn.* 158: 679–685.
Conover, M. R., Miller, D. E., & Hunt, G. L. 1979. Female-female pairs and other unusual reproductive associations in Ring-billed and California Gulls. *The Auk* 96: 6–9.
Fisher, J. 1952. *The Fulmar*. Collins, London.
Grealy, A., Bunce, M., & Holleley, C. E. 2019. Avian mitochondrial genomes retrieved from museum eggshell. *Mol. Ecol.* 19: 1052–1062.
Hunt, G. L., & Hunt, M. W. 1977. Female-female pairing in Western Gulls (*Larus occidentalis*) in Southern California. *Science* 196: 1466–1467.
Jensen, J-K. 1989. Toægs-kuld hos færøske Mallemukker. [Two-egg clutches of Fulmars in the Faroes]. *Dansk Ornitologisk Forenings Tidsskrift* 83: 83–88.
— 2012. *Mallemukken på Færøerne.* [The Fulmar on the Faroe Islands]. Torshavn.
Jones, A. G., & Ardren, W. R. 2003. Methods of parentage analysis in natural populations. *Mol. Ecol.* 12: 2511–2523.
Lockley, R. M. 1936. On the breeding birds of the Westmann Islands. *Ibis* 13: 712–718.
Michel, P., & Thompson, P. M. 2003. A simple photogrammetric technique for estimating egg volume from field measurements. *Atlantic Seabirds* 5: 31–34.
—, Ollason, J. C., Grosbois, V., & Thompson, P. M. 2003. The influence of body size, breeding experience and environmental variability on egg size in the Northern Fulmar (*Fulmarus glacialis*). *J. Zool.* 261: 427–432.
Mónus, F., & Barta, Z. 2005. Repeatability analysis of egg shape in a wild Tree Sparrow (*Passer montanus*) population: a sensitive method for egg shape description. *Acta Zoologica Academiae Scientarium Hungaricae* 51: 151–162.
Petersen, M. R. 1992. Intraspecific variation in egg shape among individual Emperor Geese. *J. Field Ornithol*. 63: 344–354.
Romanoff, A. J., & Romanoff, A. L. 1949. *The Avian Egg*. Wiley, New York.
Ryan, P. G., Cuthbert, R., & Cooper, J. 2007. Two-egg clutches among albatrosses. *Emu* 107: 210–213.
Tickell, W. L. N., & Pinder, R. 1966. Two-egg clutches in albatrosses. *Ibis* 108: 126–129.
Waits, L. P., Luikart, G., & Taberlet, P. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Mol. Ecol.* 10: 249–256.
Warham, J. 1990. *The Petrels: their ecology and breeding systems*. Academic Press, London.

T. R. Birkhead and J. E. Thompson, Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN; e-mail T.R.Birkhead@sheffield.ac.uk
J-K. Jensen, I Geilini 37, FO-270 Nolsoy, Faroe Islands
S. Hammer, Environment Agency, Traðagøta 38, FO-165, Argir, Faroe Islands
P. M. Thompson, Lighthouse Field Station, George Street, Cromarty, Ross-shire IV11 8YJ
R. Montgomerie, Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada

The authors are an eclectic collection of Fulmar enthusiasts from the UK, the Faroes and Canada.

APPENDIX 3:

New insights from old eggs – the shape and thickness of Great Auk *Pinguinus impennis* eggs

New insights from old eggs – the shape and thickness of Great Auk *Pinguinus impennis* eggs

Birkhead, T. R., Russell, D. G. D., Garbout, A., Attard, M. R. G., Thompson, J. E. and Jackson, D. (2020). *Ibis*, **Early view**, doi: 10.1111/ibi.12820.

Original article and Supplementary Materials can be found using the link below:

https://onlinelibrary.wiley.com/doi/full/10.1111/ibi.12820

Paper context and thesis author's contributions: The Great Auk is an extinct close relative of the Razorbill and two *Uria* species (Common and Brünnich's Guillemot). Whilst there are various historical accounts of the Great Auk, we know surprisingly little about the breeding behaviour and environment of this extinct species. In **Chapters 4-8** we have highlighted how several egg traits, specifically for the Common Guillemot, are driven by unique adaptive pressures in the incubation environment. Considering these findings, we aimed in this study to quantify and compare certain traits of Great Auk eggs with those of the closely related Razorbill, Common Guillemot and Brünnich's Guillemot, in order to try and speculate the potential incubation behaviours and environments that the Great Auk might have possessed. To do this we (i) quantified (using methods presented in **Chapter 2**) and compared egg shape, as well as (ii) quantified and compared eggshell thickness measurements of Great Auk eggs to those of the other three closely related extant auk species.

My contribution to this published article comprised of obtaining measurements and photographs of eggs sourced from museums and fieldwork (obtained under licence), in addition to extracting and processing images of Great Auk eggs from a book source, for shape analysis. All automated shape analysis script runs on egg images were conducted by myself. I collated the egg shape dataset and, for this data, produced all the statistical analyses and figures included in the published manuscript. I performed stability tests on model Great Auk and Brünnich's Guillemot model eggs and collated and analysed the data for these experiments. I contributed suggestions and improvements to subsequent re-drafts of the manuscript.

Co-authors' contributions: T.R. Birkhead conceived the idea for the study. T.R. Birkhead did the research for the study and wrote the initial draft of the manuscript. All co-authors contributed suggestions and improvements to subsequent re-drafts of the manuscript. D.G.D. Russell gained necessary permissions to scan Great Auk eggs, with the initial assistance of M.R.G. Attard. D.G.D. Russell and D. Jackson developed methods for safely micro-CT scanning the Great Auk eggs. A. Garbout conducted the micro-CT scans with assistance from D. Jackson. D. Jackson processed all micro-CT scanning images and obtained and analysed effective eggshell thickness measurement data. T.R. Birkhead assisted with the collection of egg measurements for the shape analysis dataset.

IBIS
BOU international journal of avian science
Ibis (2020) doi: 10.1111/ibi.12820

Short communication

New insights from old eggs – the shape and thickness of Great Auk *Pinguinus impennis* eggs

TIM BIRKHEAD*[1] DOUGLAS RUSSELL,[2] AMIN GARBOUT,[3] MARIE ATTARD[4] JAMIE THOMPSON[1] & DUNCAN JACKSON[1]
[1]*Department of Animal & Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK*
[2]*Bird Group, Department of Life Sciences, Natural History Museum, Akeman Street, Tring, HP23 6AP, UK*
[3]*BMNH, South Kensington, London, SW7 5BD, UK*
[4]*Department of Biological Sciences, Royal Holloway University of London, Egham Hill, Egham, Surrey, TW20 0EX, UK*

We compared the shape and eggshell thickness of Great Auk *Pinguinus impennis* eggs with those of its closest relatives, the Razorbill *Alca torda*, Common Guillemot *Uria aalge* and Brünnich's Guillemot *Uria lomvia*, in order to gain additional insights into the breeding biology of the extinct Great Auk. The egg of the Great Auk was most similar in shape to that of Brünnich's Guillemot. The absolute thickness of the Great Auk eggshell was greater than that of the Common Guillemot and Razorbill egg, which is as expected given its greater size, but the relative shell thickness at the equator and pointed end (compared with the blunt end) was more similar to that of the Common Guillemot. On the basis of these and other results we suggest that Great Auk incubated in an upright posture in open habitat with little or no nest, where its pyriform egg shape provided stability and allowed safe manoeuvrability during incubation. On the basis of a recent phylogeny of the Alcidae, we speculate that a single brood patch, a pyriform egg and upright incubation posture, as in the Great Auk and the two *Uria* guillemots, is the ancestral state, and that the Razorbill – the Great Auk's closest relative – secondarily evolved two brood patches and an elliptical egg as adaptations for horizontal incubation, which provides flexibility in incubation site selection, allowing breeding in enclosed spaces such as crevices, burrows or under boulders, as well as on open ledges.

Keywords: Alcidae, egg shape, eggshell thickness, pyriform.

The Great Auk *Pinguinus impennis* is extinct. What are thought to have been the last two individuals were killed on the island of Eldey, Iceland, in June 1844 (Grieve 1885, Newton 1896, Fuller 1999). Since then, attempts have been made to reconstruct aspects of the Great Auk's life history from two main sources: (1) anecdotal accounts of live birds observed at their breeding colonies only by those intent on harvesting the birds and their eggs rather than by scientists, and (2) the ~80 skins, skeletal material and alcohol-preserved internal organs of two individuals, as well as ~70 eggs, most of which now exist in museum collections (Bengtson 1984, Fuller 1999). This material is all that is available for reconstructing the life of the Great Auk – albeit with the help of new technologies (e.g. Thomas *et al.* 2017).

The Great Auk was a member of the Alcidae (auks) but was unique among contemporaneous alcids in being flightless. The living Alcidae comprise at least 24 species in 10 genera that separate into at least two distinct groups in six tribes. Recent phylogenetic analysis identifies the Great Auk and the Razorbill *Alca torda* as sister species within Tribe Alcini with a common ancestor about 11 million years ago (mya). The two *Uria* guillemots (Common Guillemot *Uria aalge* and Brünnich's Guillemot *Uria lomvia*: known as Common Murre and Thick-billed Murre, respectively, in North America) are sister species with a common ancestor some 7 mya, with all four species having a common ancestor about 17 mya (Smith & Clarke 2015).

Much has been written about the Great Auk, but several aspects of its breeding biology and life history remain a mystery (Newton 1896, Bengtson 1984, Harris & Birkhead 1985). However, it is known that the Great Auk was confined to the North Atlantic where, like many other seabirds, it bred colonially, mainly on offshore islands. Like the Razorbill and the two guillemots, the Great Auk produced a single-egg clutch. The two guillemots have, and the Great Auk had, a single, centrally placed brood patch, whereas the Razorbill, despite its single-egg clutch, has two lateral brood patches (Bengtson 1984, Harris & Birkhead 1985).

The characteristics of a species' eggs, such as shape and eggshell thickness, can provide an indication of the ecological conditions in which that species lays and incubates its egg(s) (Birkhead *et al.* 2019) and hence an opportunity to obtain new insights into the breeding ecology of the Great Auk.

Egg shape may tell us something about the situation in which the Great Auk laid and incubated its egg (see Birkhead 1993, Montevecchi & Kirk 2020). Like the Common Guillemot and Brünnich's Guillemot, the Great Auk egg has been described as 'pyriform', or pear-shaped, with

---

*Corresponding author.
Email: T.R.Birkhead@sheffield.ac.uk

one very pointed end (Walters 1994). The Razorbill, despite its closer phylogenetic affinity to the Great Auk compared with the *Uria* guillemots, produces an egg whose shape is much less pointed, often described as 'elliptical ovate to elongate ovate' (Bent 1919: 203, see also Harris & Birkhead 1985: 174). A pyriform-shaped egg is one that is relatively elongate, relatively asymmetric and much more pointed at one end than the other (Thomson 1964, Biggins *et al.* 2018). This extreme among avian egg shapes has long been considered difficult to quantify (see Biggins *et al.* 2018). In contrast, the shape of most other bird eggs can be adequately described by two indices: elongation (length relative to breadth) and asymmetry (the length from the egg's widest point to the most pointed end, divided by the overall length; called 'Pointedness' in Biggins *et al.* 2018). Variants of these indices in different studies have been identified and defined in Biggins *et al.* (2018). However, the two indices, elongation and asymmetry, do not adequately capture the shape of pyriform eggs (e.g. Stoddard *et al.* 2017). To deal with this, Biggins *et al.* (2018) used a third index, polar asymmetry (see below).

Recent studies of the Common Guillemot egg show that its pyriform shape confers stability and it is less likely to be dislodged on a sloping substrate than would a more typically shaped avian egg (Birkhead *et al.* 2019). This stability in turn seems likely to increase the control that incubating birds have over the egg's movement, for example during egg turning and incubation change-overs, and when birds incubate in an upright posture with no nest (Birkhead *et al.* 2018, 2019).

Eggshell thickness may provide information relating to the substrate on which Great Auk eggs were incubated. For example, a comparison between the Common Guillemot and Razorbill (Birkhead *et al.* 2017a) showed that the region below the equator (adjacent to the pointed end of the egg) of the Common Guillemot egg is relatively thicker than that of the Razorbill. This difference may relate to egg size or shape, with the more elongate (and hence weaker) shape of Guillemot eggs requiring reinforcement at the equator (Maurer *et al.* 2012). Guillemots breed at high density and incubate on bare rock where the risk of physical damage to the egg is high and the greater thickness and hence strength of this part of the eggshell may reinforce a region that lies in contact with the substrate and where damage is most likely to occur (Belopol'skii 1957, Uspenski 1958, Birkhead *et al.* 2017a). A comparison of the thickness of the different regions of Great Auk eggs with other alcids may therefore allow us to infer something about the risks of damage and hence the breeding situation.

Recent developments in (1) accurately quantifying avian egg shape (Biggins *et al.* 2018), (2) interpreting the adaptive significance of egg shape (Stoddard *et al.* 2017, Deeming 2018, Birkhead *et al.* 2018, 2019) and (3) micro-computed tomography (micro-CT) techniques for visualizing and measuring the thickness of avian eggshells (Riley *et al.* 2014, Birkhead *et al.* 2017a, Jackson *et al.* 2018) provide the opportunity to obtain new data from Great Auk eggs. Our overall aim was to compare the shape of and the variation in shell thickness along the length of Great Auk eggs with those of the Common Guillemot, Brünnich's Guillemot and Razorbill, in the hope of obtaining a better understanding of the breeding biology of the Great Auk.

METHODS

Egg shape

We quantified egg shape using the methods described by Biggins *et al.* (2018), which provide three indices of shape:

- Elongation: the ratio of the length to the width at the widest point
- Asymmetry (pointedness): the length from the point where the egg is widest to the more distant end divided by the overall length
- Polar asymmetry: the ratio of the diameter of the largest circle that will fit within the egg outline and touch the egg at its blunt pole to the diameter of the largest circle within the egg outline and touching the more pointed pole.

Indices of egg shape were obtained from photographs taken under standardized conditions (Birkhead *et al.* 2017a, 2017b) for all eggs except those of the Great Auk, which were obtained from photographs in Tomkinson and Tomkinson (1966); as described elsewhere (Birkhead *et al.* 2019) we verified that these photographs were completely appropriate for shape analyses. Eggs of Common Guillemots and Razorbills were either from museum collections and/or collected under licence in the field between 2014 and 2016 (and then placed in a museum collection). The three scanned Great Auk eggs were from the Natural History Museum, Tring, UK. Sample sizes for egg shape indices were as follows: Razorbill (n = 101, comprising 10 and 17 from Skomer Island in 2015 and 2016, respectively, and 74 from museums, all from Bempton Cliffs, Yorkshire), Great Auk (n = 51 from Tomkinson & Tomkinson 1966), Common Guillemot (n = 735, comprising 98, 62 and 54 from Skomer Island in 2014, 2015 and 2016, respectively, and 521 from museums, collected over their entire distribution range) and Brünnich's Guillemot (n = 296, all from museum collections, collected over their entire distribution range) (see also Birkhead *et al.* 2019, Appendix S1).

Although we previously found a (weak) relationship between egg volume and shape (Birkhead *et al.* 2017a), in the present study we did not control for egg volume in our analyses of egg shape primarily because we were interested in using egg shape to infer something about the ecology and breeding site of the Great Auk in terms of the stability of its egg (see below and Appendix S1).

Stability

It has recently been shown that the most likely benefit of a pyriform shape in the Common Guillemot egg is that it confers stability by maximizing the surface area of the egg in contact with the substrate, such that the egg is more easily and more swiftly positioned in a stable stationary position and therefore is inherently less likely to be dislodged on a sloping surface (Birkhead *et al.* 2018). Given the similar pyriform shape of Great Auk eggs to those of the two guillemot species, it is predicted that their shape will also confer some stability. What is not known is whether the greater size (and fresh mass, estimated to be 327 g, cf. Common Guillemot: ~110 g; Brünnich's Guillemot ~100 g; Razorbill ~90 g – all values from Harris & Birkhead 1985) of a Great Auk egg influences its stability.

To establish the extent to which the shape and mass of the Great Auk egg confer stability, it is impossible to use real 'live' eggs. We therefore created 10 pairs of three-dimensional (3-D) printed eggs (using shape measurements based on 10 real Great Auk eggs (Appendix S2), one the size and shape of a Great Auk egg and one exactly the same shape but the size of a Brünnich's Guillemot egg) in order to check that mass did not affect stability. To simulate the consistency of fresh eggs, we included an appropriately sized air cell at the blunt pole and then completely filled the remaining space in the egg with albumen from chicken eggs. The mass (mean ± sd) of the filled eggs was 312.90 ± 37.70 g for Great Auk and 82.00 ± 5.10 g for Brünnich's Guillemot. We used Brünnich's Guillemot egg size as a comparison because it had previously been suggested that these eggs were more similar in shape to Great Auk eggs than are Common Guillemot eggs (Harris & Birkhead 1985), as we confirmed (see below). We then subjected each egg to exactly the same tests, using the identical methods that we had used previously in a comparison of the stability of Common Guillemot and Razorbill eggs, establishing the steepest slope upon which an egg would remain stable, on either a moving (i.e. gradually increasing) slope or a static slope (see Birkhead *et al.* 2017b) (for details see Appendix S2).

Eggshell thickness

We used micro-CT to visualize and quantify the thickness of eggshells in three different regions of the egg: (1) adjacent to the blunt pole, (2) just below the equator towards the pointed pole and (3) adjacent to the pointed pole. Our measure of eggshell thickness was 'effective eggshell thickness', which is the distance between the point of fusion of the palisade columns to the outer surface of the shell accessory material, which is likely to be the most important aspect of shell thickness for eggshell strength (Bain 2005, Solomon 2010, Birkhead *et al.* 2017a) (Fig. 2). Effective shell thickness is positively correlated with both trueshell thickness (i.e. the calcium carbonate shell and any shell accessory material) and total shell thickness (i.e. all shell layers including the organic membranes; see Birkhead *et al.* 2017a). We examined thickness in the three different regions of each species' egg relative to each other (as in Birkhead *et al.* 2017a) (Fig. 2). Sample sizes were as follows: Razorbill (10, $n = 5$ three replicates per region per egg, $n = 5$ one replicate per region per egg), Great Auk (3, three replicates per region per egg) and Common Guillemot (10, $n = 5$ three replicates per region per egg, $n = 5$ one replicate per region per egg). Repeatabilities of egg thickness measurements are given in Appendix S3. The data on Common Guillemot and Razorbill eggs are from Birkhead *et al.* (2017a). For these comparisons we did not have access to shell material for Brünnich's Guillemot eggs. CT scanning of the two guillemot and Razorbill egg shells was conducted as described earlier using fragments of shell (Birkhead *et al.* 2017a), but the Great Auk eggs were scanned whole, mounted in protective casings, as described by Russell *et al.* (2018). The sample size for the Great Auk is small because of the time required (and the concomitant cost) to scan entire eggs. The CT scanner and settings used for the Great Auk eggs were as described in Appendix S3.

RESULTS

Shape

All three shape parameters (asymmetry/pointedness, elongation and polar asymmetry) were statistically different across the four auk species in multivariate testing (multivariate analysis of variance (MANOVA): Wilks' lamba = 0.56, $F_{9,\ 2864.7} = 84.45$, $P < 0.0001$). Considered separately, the overall differences among the four species also differed significantly for each of the three shape indices (analysis of variance (ANOVA), asymmetry/pointedness: $F_{3,\ 1179} = 257.4$, $P < 0.0001$; elongation: $F_{3,\ 1179} = 44.81$, $P < 0.0001$; polar asymmetry: $F_{3,\ 1179} = 78.98$, $P < 0.0001$). However, post-hoc Tukey tests highlighted that whereas all other paired species comparisons showed significant differences in egg shape, the Great Auk and Brünnich's Guillemot paired species comparisons showed no significant differences between any of the three shape indices (asymmetry/pointedness: $P = 0.924$; elongation: $P = 0.582$; polar asymmetry: $P = 0.408$; see Fig. 1 and Appendix S4). These results

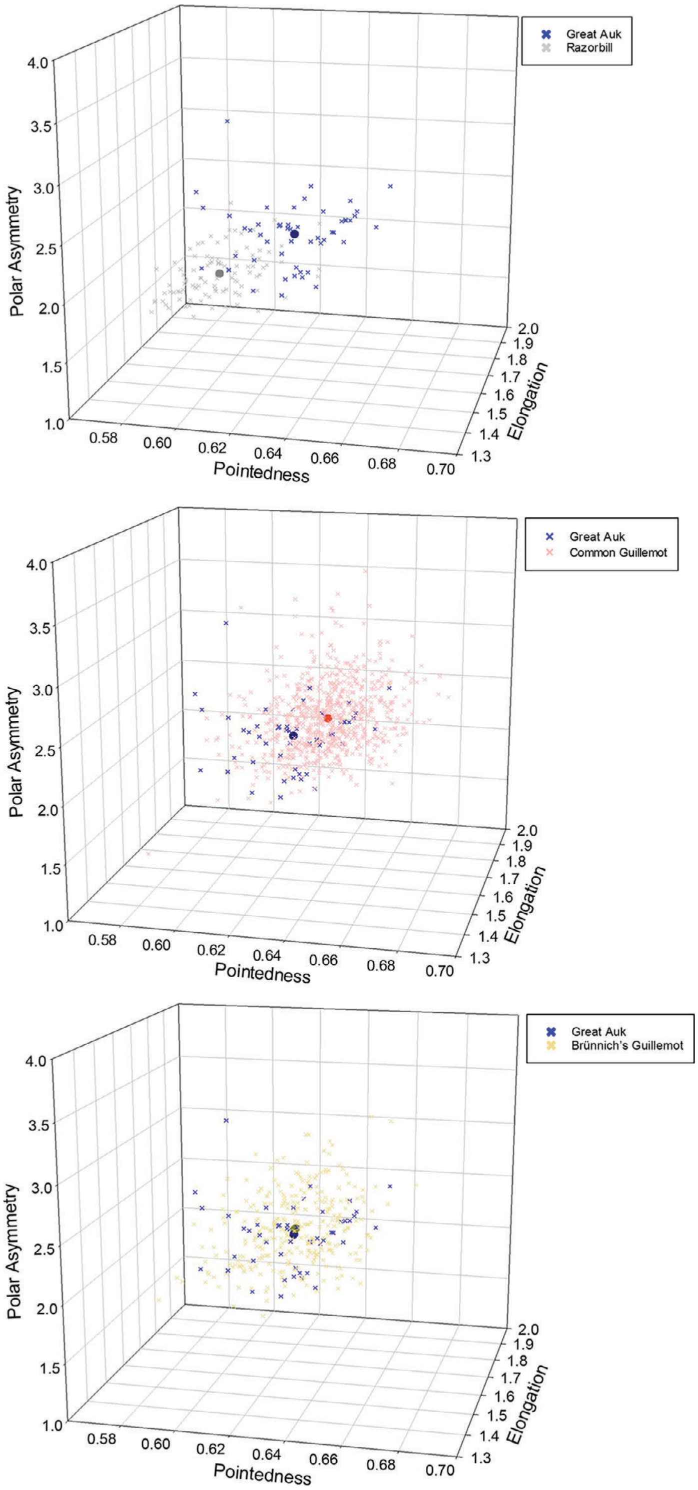


Figure 1. 3-D plots of three egg shape indices (elongation, pointedness and polar asymmetry derived, see Biggins et al. 2018), separately comparing the Great Auk, with Razorbill, Common Guillemot and Brünnich's Guillemot.

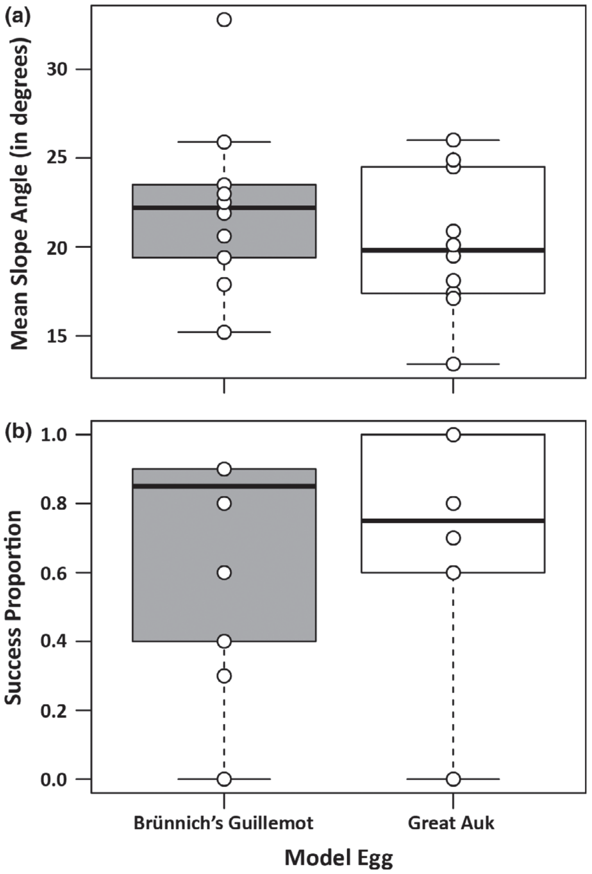


Figure 2. Comparisons between a typical Brünnich's Guillemot-sized and Great Auk-sized 3D-printed model eggs of identical shape for (a) mean slope angle reached in the moving slope experiment and (b) the success proportion obtained in the static slope experiment. Comparisons were based on 10 pairs of eggs. The purpose of these tests was to assess the stability of eggs of identical shape but different sizes. These tests should not be compared with similar stability tests performed in Birkhead *et al.* (2018) where real eggs were tested. Boxes are the interquartile range, black line within the box is the median, and the whiskers show the highest and lowest values (excluding outlier data points). Black circles with no fill are the individual data points. The differences between the two egg sizes for each experiment are not statistically significant (see text) (see Appendix S2).

therefore highlight that Great Auk eggs are most similar to Brünnich's Guillemot eggs in terms of their shape (Fig. 1, Appendix S4).

Stability

We found no difference in the maximum slope at which a model Great Auk egg or a Brünnich's Guillemot-sized egg would remain stable (Fig. 2; mean slope angle ± sd, Great Auk: 20.19 ± 3.99° and Brünnich's Guillemot: 22.27 ± 4.79°; paired *t*-test: $t = 1.18$, df = 9, $P = 0.269$; Appendix S2) or a static slope of 35° (mean success proportion ± sd, Great Auk: 0.65 ± 0.37 and Brünnich's Guillemot: 0.66 ± 0.32; paired *t*-test: $t = 0.17$, df = 9, $P = 0.868$) (Fig. 2).

Eggshell thickness

Overall, and not surprisingly given its greater egg and body size, the eggshell of the Great Auk egg was absolutely thicker, in terms of effective thickness, than that of the Common Guillemot, which in turn was thicker than that of the Razorbill (Fig. 3, MANOVA: Pillai's trace = 1.04, $F_{6,38} = 6.91$, $P < 0.0001$; separate one-way ANOVAs for each region, blunt end: $F_{2,20} = 56.6$, $P < 0.0001$; equator: $F_{2,20} = 243.7$, $P < 0.0001$; pointed end: $F_{2,20} = 76.1$, $P < 0.0001$; all multiple comparisons between species at each egg region were significant; $P < 0.05$). In all three species, the equator was thicker than the blunt end. In both the Great Auk and the Common Guillemot, the two regions sampled below the egg's widest point were relatively thicker than in the Razorbill (Fig. 3). One can also consider these results the other way: that in the Great Auk and in the Common Guillemot egg, the blunt pole of the egg was relatively thinner than the equator/pointed end in the Razorbill egg.

DISCUSSION

The Great Auk egg is more similar in shape to that of the two guillemots, and in particular Brünnich's Guillemot, than to the Razorbill, to which it is phylogenetically closest. The eggshell of the Great Auk is absolutely thicker than that of either the Common Guillemot or their Razorbill egg, and although we did not have the material to measure it directly, also thicker than Brünnich's Guillemot egg (see Uspenski 1956: 41), undoubtedly because of the greater size of the Great Auk egg (Ar *et al.* 1974, Rahn & Paganelli 1989).

Although the sample sizes for the Great Auk were small, our results (see Fig. 2) indicate that the differences in thickness within Great Auk eggs are similar to but more pronounced than in the Common Guillemot and the Razorbill (and also Brünnich's Guillemot – see Uspenski 1956 for measures of total shell thickness). However, a larger sample size would be needed to test this observation rigorously. The observed differences in eggshell thickness may be a consequence of the Great Auk (1) laying an elongate egg, which as a result was weaker along its long axis; (2) laying an absolutely larger egg; (3) being up to five times heavier than a guillemot or Razorbill egg and hence increasing the weight the egg has to support during incubation; and (4) potentially incubating its egg on a hard surface and therefore

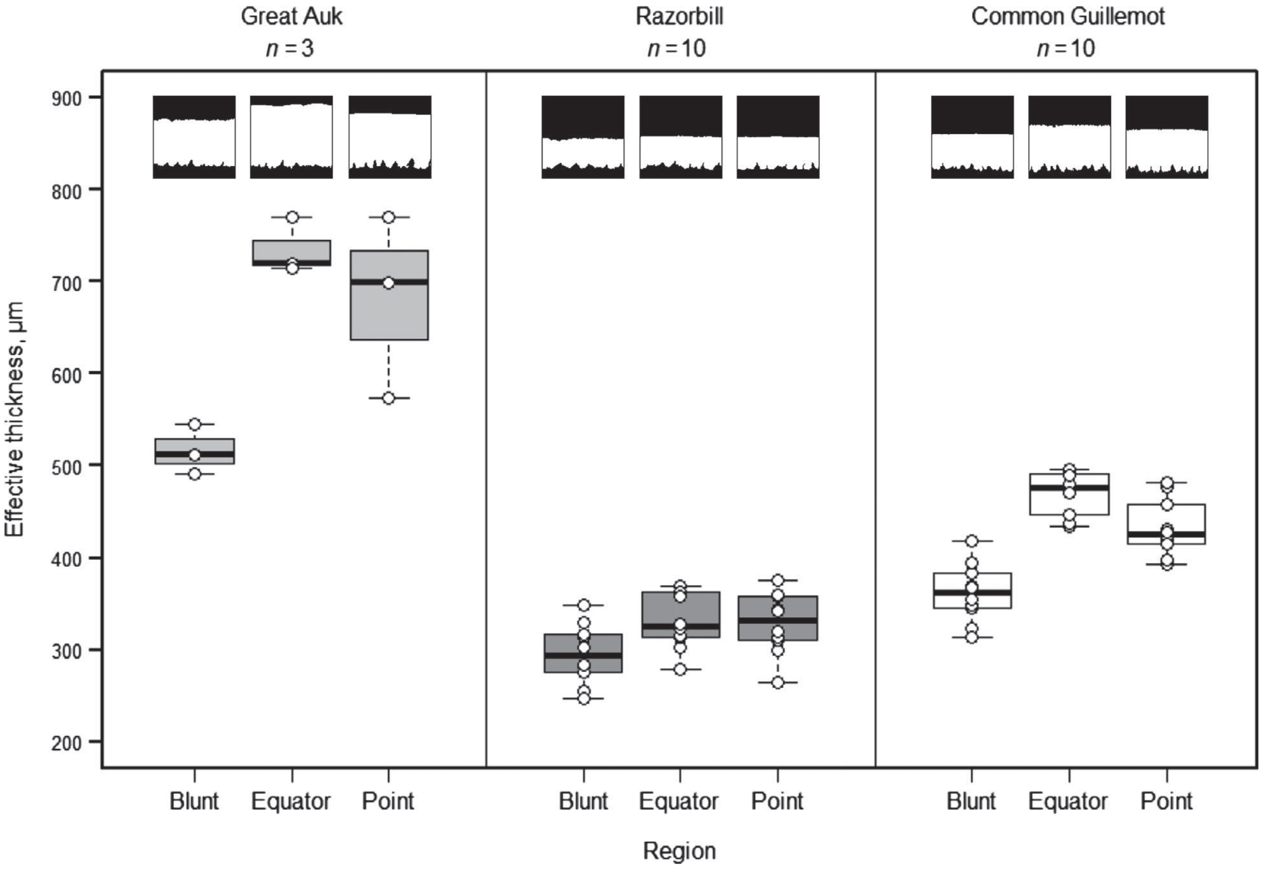


Figure 3. Effective eggshell thickness for three different regions (blunt end, equator and pointed end) of Great Auk, Razorbill and Common Guillemot eggs. Differences between regions are significant in all three species (see Appendix S3 for statistical comparisons). Examples of variation in shell thickness along a single egg (selected to represent the median closely) for each species are shown above the box plot; each square is 1 mm long (see Appendix S3, Fig. A3.1 for details).

requiring reinforcement in the region where the egg is in contact with the brood patch and substrate (Belopol'skii 1957, Uspenski 1958, Birchard & Deeming 2009, Maurer *et al.* 2012). The relatively thin blunt end of the Great Auk egg may facilitate hatching – assuming the Great Auk is like most other birds, including the guillemots and Razorbill – by pipping at and emerging from the blunt end of the egg (Tschanz 1968), from an egg whose shell is otherwise fairly robust.

The fact that the average shape of the Great Auk egg is virtually identical to that of an average Brünnich's Guillemot egg suggests that the Great Auk egg would have had similar stability and 'safe manoeuvrability' to that of a Brünnich's Guillemot egg, and greater stability than a Razorbill egg, but perhaps less than a Common Guillemot egg, which is often more pyriform (Fig. 1; and Birkhead *et al.* 2018). Our results using 3-D printed eggs strongly suggest that eggs of identical pyriform shape but different mass have similar stability on sloping surfaces.

We have previously suggested that in the alcids, a pyriform-shaped egg and a single, centrally positioned brood patch facilitate an upright or semi-upright incubation posture that may be an adaptation to breeding on bare, open habitat with no nest (Birkhead 1993, Birkhead *et al.* 2019). The Razorbill, by contrast, has a more rounded, elliptical shaped egg, two lateral brood patches and incubates in a horizontal position. Both guillemot species incubate their egg with the blunt end oriented forwards, lying between (but not on) the legs, resting on the substrate or partially on the foot webs. An upright posture may also facilitate high-density breeding in Common Guillemots, which breed at higher densities than Brünnich's Guillemots and incubate in a more upright posture (Spring 1971). There are no descriptions of undisturbed, incubating Great Auks, but their single, central brood patch suggests that, like the guillemots *Uria* spp., this species may also have incubated in an upright position (Birkhead 1993).

Five additional factors could potentially explain the evolution of the Great Auk's pyriform egg.

- Minimizing the likelihood of dirt contamination of the egg's blunt end, as in the Common Guillemot, whose pyriform egg lies at an angle with its long, straight edge horizontal to and in direct contact with the substrate, such that its blunt end is free from any dirt on the substrate (see Fig. 1 in Birkhead *et al.* 2017a).
- A pyriform shape may confer greater strength and resistance to impacts during incubation (see Birkhead *et al.* 2017a). This idea has proved challenging to test (T. R. Birkhead, J. E. Thompson & M. Attard unpubl. results) because of the difficulty of separating the effects of shape from eggshell thickness in conferring strength.
- Johnson (1941) suggested that for Common Guillemots a pyriform egg, together with upright incubation, would result in a greater surface area of the egg in contact with the brood patch and more efficient incubation. Our attempts to test this using 3-D printed eggs matched for mass and the thermal properties of real Common Guillemot eggs revealed that the brood patch was so efficient at warming eggs of different shapes that the idea that a pyriform egg facilitates more efficient incubation seems unlikely (T. R. Birkhead and J. E. Thompson unpubl. results).
- Birds laying relatively larger eggs are more likely to produce eggs that are more elongate and asymmetric in shape (Stoddard *et al.* 2017, Deeming 2018). In Stoddard *et al.*'s study (2017: Table S2B,C in Appendix S2) egg size and female body size accounted for 29–47% of the explained variation in egg shape (ellipticity and asymmetry), with an additional 4–5% of the explained variation accounted for by 'flight efficiency'. Birds are able to produce eggs that are relatively much larger (up to 29% of female body mass: Warham 1990) than the neonates of mammals (or the eggs of dinosaurs) because, unlike mammals (and dinosaurs), most birds have an open pelvis (Deeming 2018). However, there must be some constraints on avian egg diameter, as the way birds produce relatively larger eggs is – apparently – to produce relatively elongate eggs (although it is not clear why relatively larger eggs tend also to be more asymmetric). We can probably discount the idea that the Great Auk's pyriform egg (which is both relatively elongate and asymmetric) is solely a consequence of its size, because, although large in absolute terms, it is relatively the smallest egg among alcids, constituting just 7% of estimated female body mass (compared with 11–12% for the two guillemots and the Razorbill and over 20% in the Ancient Murrelet *Synthliboramphus antiquus* and Guadalupe (Xantus') Murrelet *Synthliboramphus hypoleucus*; Gaston & Jones 1998; Birkhead *et al.* 2018). Yet, in auks and penguins absolutely larger eggs tended to be more pyriform, so we cannot rule out that the Great Auk egg is more asymmetric and elongate with high polar asymmetry, because – at least in part – its egg is absolutely large. As incubation site alone explained 65% of the variation in egg-shape indices across the auks and penguins (Birkhead *et al.* 2019), it is likely to be relatively more important than egg size in the evolution of egg shape in the Great Auk.
- Stoddard *et al.* (2017) and Deeming (2018) reported that some of the variation in avian egg shape is associated with developmental mode (or some correlate of it, such as relative egg size, as discussed above). It is generally assumed that, like its closest relatives the Razorbill and the two guillemots, Great Auk chicks had an 'intermediate' mode of development and departed from the colony at about 20% of adult body mass at 17–21 days of age (compared with precocial alcids such as the Ancient Murrelet, whose chicks depart after 2 days or, at the other extreme, the semi-precocial Atlantic Puffin *Fractercula arctica*, whose chick departs after 40 days) (Gaston & Jones 1998, Houston *et al.* 2010, Birkhead *et al.* 2018). It seems unlikely that developmental mode explains the pyriform egg of the Great Auk, as across species (including auks) precocial and semi-precocial chicks hatch from both pyriform and non-pyriform eggs (Birkhead *et al.* 2018).

Like the two guillemots, Great Auks also bred in the open and at high density, and as far as is known, with no nest of any kind (Bengtson 1984, Montevecchi & Kirk 2020). The fact that Great Auk eggs exhibit such enormous variation in the pattern, distribution and density of their maculation (see images in Tomkinson & Tomkinson 1966, Fuller 1999) is consistent with the idea that, like the two guillemots, eggs laid in close proximity risked becoming mixed up, and a unique maculation signature may have enabled parents to recognize and retrieve their own egg (see Tschanz 1968).

The best evidence that Great Auks bred at high density is the surveyor Taverner 1718 report from Penguin Islands, Newfoundland: 'They [the French inhabitants of Placentia, Newfoundland] told me that a Mann, could not goe ashoar upon those islands, without Bootes, for otherwise they would spoile his Leggs, that they were Intirely covred with those fowles, soe close that a Mann could not put his foot between them' (cited in Montevecchi & Kirk 2020).

While Taverner's statement clearly indicates that Great Auks bred at high density, it could be interpreted in two ways: literally, indicating that Great Auks bred in direct bodily contact with one another like Common

Guillemots, in which case adjacent eggs might be as little as 30 cm apart, or as a slight exaggeration, as was common when describing, for example, the abundance of seabirds, indicating that Great Auks bred close together but not in bodily contact. Given that Great Auks were flightless, they had to walk to reach their individual breeding sites, which would have meant finding a way between other breeding individuals, and hence that some spacing existed between breeding pairs.

Common Guillemots benefit from breeding at high density, as this allows them to protect their eggs and chicks from predators such as gulls and corvids (Birkhead 1977). It may not have been necessary for Great Auks to breed in direct contact with conspecifics to protect their eggs and chicks from predators, for two reasons. The Great Auks' large body size (~70 cm tall; Bengtson 1984: estimated mass 5000 g, Bédard 1969), compared with guillemots *Uria* spp. ~30 cm tall and ~1000 g body mass), means that Great Auks were probably better able to defend their eggs and chicks from aerial predators, in part because they were stronger and could potentially inflict greater damage on these predators (maximum body mass for Great Black-backed Gull *Larus marinus* is 2300 g) than can the two guillemots *Uria* or the Razorbill, and predators may therefore have been more reluctant to risk injury. In addition, when gulls or corvids take guillemot or Razorbill eggs from the incubating parent birds, they do so warily and by rapid snatching (to avoid being injured by the parent), grasping the egg at its maximum diameter in their bill. The Great Auk's larger egg (mean maximum width ~75 mm) would have been relatively difficult for gulls and ravens to grasp, so their actively incubated eggs were probably less vulnerable to gull and corvid predation than those of guillemots *Uria* spp. and the Razorbill (Appendix S5).

One puzzle remains. It is generally accepted that the Great Auk's closest relative is the Razorbill. Indeed, the two species are very similar in their physical conformation (even though the Great Auk is considerably larger) and phylogenetic analyses place the two as sister species (Smith & Clarke 2015). It is somewhat surprising therefore that the Great Auk exhibits several traits – including its egg shape – that are more similar to the two *Uria* guillemots than to the Razorbill. A possible explanation for this relates to the brood patch. Superimposing the number of brood patches (one or two) onto Smith and Clarke's (2015) phylogeny suggests that a single brood patch, a pyriform egg and upright incubation posture (as in the Great Auk and *Uria* guillemots) is the ancestral state and that the Razorbill secondarily evolved two brood patches and a more elliptically shaped egg, presumably as adaptations for horizontal incubation. This in turn allows the Razorbill greater flexibility in incubation site selection, allowing them to breed in relatively small enclosed spaces including crevices, under boulders and in burrows, as well as out in the open on ledges. Other alcids (auklets and puffins) that lay a single egg and incubate in a crevice or burrow have two lateral brood patches (Gaston & Jones 1998: 26). Laterally located brood patches may be more efficient for horizontal incubation posture, and also allow the incubating alcid to position its single egg on either side of its body and hence adjust its own orientation within its breeding site.

In summary, on the basis of the shape of its egg and eggshell thickness we suggest that the Great Auk incubated in an upright posture, probably on bare rock surfaces, where its pyriform-shaped egg provided stability during incubation, and its relatively thick shell at the equator and pointed end provided protection from mechanical damage.

We thank all the museum curators for allowing us to measure and photograph the eggs in their care. We are especially grateful to Ian Owens, then Director of the Natural History Museum (London), for his support. At the Natural History Museum, Arianna Bernucci and Dr Amy Scott-Murray led in designing and building the conservation-grade system which held the Great Auk eggs within the scanner. Dr Farah Ahmed was in charge of the CT-scanning within the Natural History Museum Imaging & Analysis Centre and was the senior Natural History Museum liaison on planning and undertaking the scanning alongside Dr Amin Garbout. We thank the Wildlife Trust of South and West Wales, and Lizzie Wilberforce in particular, and Natural Resources Wales for permission to work on Skomer Island and to collect and photograph eggs there. Thanks also to Lloyd Buck for presenting his male raven, Bran, with our 3-D printed Great Auk egg and Julie Riordan and Hannah Meinertzhagen for sending us the dead Great Black-backed Gull. We are grateful to Nicola Hemmings and Bob Montgomerie for constructive comments on this paper. The study was funded by a grant from the Leverhulme Trust (to T.R.B.), a University of Sheffield Scholarship (to D.J.) and with support from the Natural History Museum. T.R.B. conceived the study and wrote the paper. D.J., J.E.T., M.A. and T.R.B. collected the data. J.E.T. made all the whole eggshell measurements and conducted and analysed the stability experiments. D.J. measured eggshell thickness. D.J. and J.E.T. analysed the data. A.G. conducted the scanning. D.J. conducted all the processing. D.R. obtained permission to move and scan the Great Auk eggs and helped to design the cradles for their scanning. J.E.T., D.J., A.G., M.A. and D.R. contributed to revising and improving the manuscript. The authors declare no competing interests.

DATA ACCESSIBILITY

The raw dataset and r-script for the statistical analyses referred to here are archived in Figshare at: https://doi.org/10.15131/shef.data.11854416.6.

REFERENCES

Ar, A., Paganelli, C.V., Reeves, R.B., Green, D.G. & Rahn, H. 1974. The avian egg: water vapour conductance, shell thickness, and functional pore area. *Condor* **76**: 153–158.

Bain, M.M. 2005. Recent advances in the assessment of eggshell quality and their future applications. *Worlds Poult. Sci. J.* **61**: 268–277.

Bédard, J. 1969. Adaptive radiation in Alcidae. *Ibis* **111**: 189–198.

Belopol'skii, L.O. 1957. *Ecology of Sea Colony Birds of the Barents Sea*. Jerusalem: Israel Program for Scientific Translations. (Translated from Russian 1961).

Bengtson, S.-A. 1984. Breeding ecology and extinction of the Great Auk (*Pinguinus impennis*): anecdotal evidence and conjectures. *Auk* **101**: 1–12.

Bent, A.C. 1919. Life histories of North American diving birds. *U.S. Nat. Mus. Bull.* **107**: 1–239.

Biggins, J.D., Thompson, J.E. & Birkhead, T.R. 2018. Accurately quantifying the shape of birds' eggs. *Ecol. Evol.* **8**: 9728–9738.

Birchard, G.F. & Deeming, D.C. 2009. Avian eggshell thickness: scaling and maximum body mass in birds. *J. Zool.* **279**: 95–101.

Birkhead, T.R. 1993. *Great Auk Islands*. London: Poyser.

Birkhead, T.R. 1977. The effect of habitat and density on breeding success in the Common Guillemot, *Uria aalge*. *J. Anim. Ecol.* **46**: 751–764.

Birkhead, T.R., Thompson, J.E., Jackson, D. & Biggins, J.D. 2017a. The point of a Guillemot's egg. *Ibis* **159**: 255–265.

Birkhead, T.R., Thompson, J.E. & Biggins, J.D. 2017b. Egg shape in the common guillemot *Uria aalge* and Brünnich's guillemots *U. lomvia*: not a rolling matter? *J. Ornithol.* **158**: 679–685.

Birkhead, T.R., Thompson, J.E. & Montgomerie, R. 2018. The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *Auk* **135**: 1020–1032.

Birkhead, T.R., Thompson, J.E., Biggins, J.D. & Montgomerie, R. 2019. The evolution of egg shape in birds: selection during the incubation period. *Ibis* **161**: 605–618.

Deeming, D.C. 2018. Effect of composition on shape of bird eggs. *J. Avian Biol.* **49**: 1–7.

Fuller, R. 1999. *The Great Auk*. Southborough: Privately Published.

Gaston, A.J. & Jones, I. 1998. *The Auks*. Oxford: Oxford University Press.

Grieve, S. 1885. *The Great Auk or Garefowl Alca Impennis, Its History, Archaeology and Remains*. London: Thomas C Jack.

Harris, M.P. & Birkhead, T.R. 1985. Breeding ecology of the Atlantic alcidae. In Nettleship, D. & Birkhead, T.R. (eds) *The Atlantic Alcidae*: 155–205. London: Academic Press.

Houston, A.I., Wood, J. & Wilkinson, M. 2010. How did the Great Auk raise its young? *J. Evol. Biol.* **23**: 1899–1906.

Jackson, D., Thompson, J.E., Hemmings, N. & Birkhead, T.R. 2018. Common guillemot (*Uria aalge*) are not self-cleaning. *J. Exp. Biol.* **221**: jeb188466.

Johnson, R.A. 1941. Nesting behavior of the Atlantic murre. *Auk* **58**: 153–163.

Maurer, G., Portugal, S.J. & Cassey, P. 2012. A comparison of indices and measured values of eggshell thickness of different shell regions using museum eggs of 230 European bird species. *Ibis* **154**: 714–724.

Montevecchi, W.A. & Kirk, D.A. 2020. Great Auk (*Pinguinus impennis*), version 1.0. In Poole, A.F. & Gill, F.B. (eds) *Birds of the World*. Ithaca, NY: Cornell Lab of Ornithology. Available at: https://birdsoftheworld.org/bow/species/greauk/1.0

Newton, A. (ed.) 1896. Gare-Fowl. In *A Dictionary of Birds*: 303–308. London: A. & C. Black.

Rahn, H. & Paganelli, C.V. 1989. Shell mass, thickness and density of avian eggs derived from tables in Schoenwetter's. *J. Ornithol.* **130**: 59–68.

Riley, A., Sturrock, C.J., Mooney, S.J. & Luck, M.R. 2014. Quantification of eggshell microstructure using X-ray micro computed tomography. *Br. Poult. Sci.* **55**: 311–320.

Russell, G.D., Bernucci, A., Scott-Murray, A., Jackson, D., Ahmed, F., Garbout, A. & Birkhead, T.R. 2018. All our eggs in one basket: challenges of high resolution x-ray micro-computed tomography of Great Auk *Pinguinus impennis* eggshell. *Biodivers. Inf. Sci. Stand.* **2**: e25794.

Smith, N.A. & Clarke, J.A. 2015. Systematics and evolution of the Pan-Alcidae (Aves, Charadriiformes). *J. Avian Biol.* **46**: 125–140.

Solomon, S.E. 2010. The eggshell: strength, structure and function. *Br. Poult. Sci.* **51**: 52–59.

Spring, L. 1971. A comparison of functional and morphological adaptations in the Common Murre (*Uria aalge*) and Thick-Billed Murre (*Uria lomvia*). *Condor* **73**: 1–27.

Stoddard, M.C., Young, E.H., Akkaynak, D., Sheard, C., Tobias, J.A. & Mahadevan, L. 2017. Avian egg shape: form, function and evolution. *Science* **356**: 1249–1254. [Supplementary Material corrected and updated 10 September 2018].

Taverner, W. 1718. Second Report relating to Newfoundland. The National Archives (PRO) CO 194/6: 226–241v [NAC MG 11, Microfilm copy, Reel B- 208].

Thomas, J.E., Carvalho, G.R., Haile, J., Martin, M.D., Samaniego Castruita, J.A., Niemann, J., Sinding, M.-H.S., Sandoval-Velasco, M., Rawlence, N.J., Fuller, E., Fjeldsa, J., Hofreiter, M., Stewart, J.R., Gilbert, M.T.P. & Knapp, M. 2017. An 'Aukward Tale': a genetic approach to discover the whereabouts of the last Great Auks. *Genes (Basel)* **8**: 164–176.

Thomson, A.L. 1964. *A New Dictionary of Birds*. Edinburgh: Nelson.

Tomkinson, P.M.L. & Tomkinson, J.W. 1966. *Eggs of the Great Auk*. London: British Museum (Natural History).

Tschanz, B. 1968. Trottellummen (*Uria aalge aalge* Pont.). *Z. Tierpsychol* **4**: 1–103.

Uspenski, S.M. 1956. *The Bird Bazaars of Novaya Zemlya. Canadian Wildlife Service Translations of Russian Game Reports*. Vol. **4**. Ottawa 159 pp (Translated from Russian 1958).

Uspenski, S.M. 1958. *The Bird Bazaars of Novaya Zemlya*. Ottawa: Department of Northern Affairs and Natural Resources, Canada. (translated from Russian).

Walters, M.P. 1994. *Birds' Eggs*. London: Dorling Kindersley.

Warham, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. London: Academic Press.

Received 4 July 2019;
revision accepted 28 January 2020.
Associate Editor: Alex Banks.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Methods: adjusting egg shape for egg size.

Appendix S2. The effect of egg size on egg stability, when shape indices are similar, using 3-D printed model eggs: a comparison of Great Auk and Brünnich's Guillemot-sized eggs.

Appendix S3. Statistical analyses of shape, effective eggshell thickness, pore density and distribution and egg surface topography across species and egg regions.

Appendix S4. Details of egg size and the statistical analyses of shape.

Appendix S5. Assessing the capabilities of typical auk egg predators to grasp a Great Auk egg in their beaks.